COMMUNITY ASSEMBLY DYNAMICS OF RAPIDS-ADAPTED FISHES OF THE XINGU RIVER

A Dissertation

by

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ABSTRACT

Increasing hydroelectric development in the tropics is beginning to place a large percentage of global freshwater diversity at risk. A prime example is the recently completed Belo Monte Hydroelectric Complex (BMHC) on the Xingu River in Brazil, which will have severe impacts on a highly endemic assemblage of rapids-adapted fishes. This dissertation uses community assembly theory as a lens to explore ecological dynamics within rapids of the Xingu prior to hydrologic alteration, with the goal of furthering empirical understanding of the assembly process, as well as providing necessary baseline data for conservation efforts. Focusing on both functional and taxonomic community structure, I use null model comparisons and multivariate statistical approaches to explore: 1) temporal dynamics between wet and dry-season assemblages, 2) variation across different functional traits, and 3) spatial variation along the impacted reach.

Significant differences in functional diversity between wet and dry-season assemblages suggest that the relative influence of community assembly mechanisms vary seasonally in response to changing abiotic conditions, with expanded habitat and decreased density of aquatic organisms during the wet season likely limiting the influence of biotic assembly mechanisms, including competitive exclusion. Significant relationships between a trait's deviation from null expectations and its correlation with trophic structure indicates that traits strongly associated with trophic ecology display

greater dispersion from the mean and more even spacing of trait values. This suggests that traits associated with trophic ecology are more influential in niche differentiation affecting species coexistence. The dominant compositional pattern observed was the high number of rapids-adapted species found upstream of the main powerhouse, further highlighting this region of the Xingu as a hotspot of aquatic diversity and identifying the area that will be dewatered by the BMHC as critically important for the conservation of this unique fauna. These results emphasize the dynamic nature of the assembly process, but suggest that traits may respond to assembly mechanisms in predictable ways. Maintenance of a dynamic flow regime that contains key components of the historic hydrograph will be critical for the conservation of this globally unique habitat and its associated diversity.

To my parents, Rita and Steve Fitzgerald, for their encouragement and love

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To the people of the Xingu who have fought to preserve this remarkable river

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CHAPTER I

INTRODUCTION

Many of the greatest threats to biodiversity, such as climate change, habitat fragmentation, and the global spread of non-native species, affect entire communities, the interactions between species, and how community-level processes impact the functioning of ecosystems (Tylianakis et al. 2008, Naeem et al. 2012). The types of species interactions within ecological communities affect the distributions and abundances of co-occurring species, and play a critical role in the maintenance of diversity (Rooney and McCann 2011). Conserving or managing biodiversity under the synergistic effects of multiple threats will increasingly require awareness of complex species interaction networks and application of the theories of community ecology (Tylianakis et al. 2010). For example, anticipating novel communities arising from species' differential response to shifting climate patterns, or managing the spread and impacts of non-native species, both require an understanding of the factors that control species co-occurrence. At the same time, many aspects of global change (*e.g.*, species introductions) can be viewed as uncontrolled experiments to test fundamental theories in community ecology (Fitzgerald et al. 2016).

Impoundments represent one of the greatest threats to aquatic biodiversity worldwide (Vörösmarty et al. 2010); their impacts on flow dynamics and river connectivity are known to affect community structure through biotic homogenization, increased invasion of exotic species, shifts towards generalist over specialist species, and

increased risk of extinction for endemics (Rahel 2000, Johnson et al. 2008, Liermann et al. 2012). Until very recently the major hotspots of aquatic diversity (Amazon, Congo, and Mekong Basins) have remained unimpeded by large dams (Liermann et al. 2012), but a recent boom in hydroelectric development in the tropics is currently threatening aquatic biodiversity on an unprecedented scale (Zarfl et al. 2015, Winemiller et al. 2016).

Perhaps the most well known of these major development projects is the 11,233 MW Belo Monte Hydroelectric Complex (BMHC) on the Xingu River in Brazil, which began generating electricity on April 20, 2016 after a long and controversial history. The BMHC will disrupt connectivity of the Amazon's largest clear-water tributary and significantly alter a 130-km stretch of rapids and anastomosing channels known as the Volta Grande. The unique design of the BMHC will divert roughly 80% of the Xingu's flow through a series of man-made canals to an off-channel powerhouse 90 m below, flooding the upstream rapids, dewatering the rapids between the diversion dam and the main powerhouse, and flooding hundreds of square-kilometers of forest outside of the river channel. Recent surveys in the impacted area have collected over 450 species of fishes in 48 families (Sabaj Pérez 2015), many of which are highly adapted to life within rapids (Zuanon 1999). Of the 63 species endemic to the Xingu Basin (Winemiller et al. 2016), at least 26 are known only from the large rapids complex in the Volta Grande region (Sabaj Peréz et al. unpublished), including the critically endangered *Hypancistrus zebra* (zebra pleco), endangered *Hopliancistrus tricornis*, and vulnerable *Ossubtus xinguense* (eagle-beaked pacu; National Red List 2016).

The rich aquatic diversity of the Xingu River and ecosystem-wide impacts of the BMHC make this a prime example of a situation in which a community-level perspective may aid conservation/management decisions. The following chapters use assembly theory as a lens to explore community dynamics of rapids-adapted fishes of the Xingu prior to hydrologic alteration, with the goal of furthering empirical understanding of the assembly process, as well as providing necessary baseline data for management. Available data on fish community structure within the region are limited to surveys of slack-water habitats and slower areas adjacent to rapids (Barbosa et al. 2015, Schmid et al. 2016). Because rapids often have distinct fauna that are particularly vulnerable to hydrologic alteration (Lujan and Conway 2015), data on the structure and dynamics of these fish assemblages throughout the impacted area are urgently needed.

Chapter II focuses on temporal dynamics, using functional diversity and null modeling approaches to test for differences in community patterns between dry- and wet-season assemblages. Despite growing interest in trait-based approaches to community assembly, little attention has been given to seasonal variation in trait distribution patterns. Mobile animals can rapidly mediate competitive interactions through dispersal, suggesting that the relative importance of assembly mechanisms can vary over short time scales in response to ontogenetic changes in dispersal or seasonal fluctuations in environmental conditions. The large seasonal variation in hydrologic conditions and species density characteristic of tropical rivers make them model systems to test for temporal variation in community assembly patterns. In addition, understanding

the seasonal dynamics of assemblages under the natural flow regime will be critical to anticipating how altered flow dynamics may impact fish assemblages.

Chapter III explores how observed patterns of functional diversity may vary across major niche dimensions within a season, focusing on traits related to habitat use or feeding strategy. Trait-based approaches to community assembly are limited by the potential for multiple deterministic assembly processes to operate along different niche axes simultaneously. Analyzing individual traits may aid understanding of assembly processes; however, single traits may influence multiple niche dimensions, complicating this approach. This chapter uses correlations with stable isotope ratios to objectively associate traits with trophic niches in order to test whether traits with higher correlations to trophic structure display greater dispersion compared to null expectations. Understanding how traits associated with different niche axes may vary in their response to multiple assembly mechanisms is a major goal of assembly theory, but may also aid in anticipating how changes to physical habitat and resource availability due to hydrologic alteration could differentially affect diversity and community structure.

Chapter IV focuses on the spatial dynamics of fish assemblages, this time using a taxonomic approach combined with multivariate methods to explore patterns of diversity within the area impacted by the BMHC. The design of the BMHC will create three distinctly altered segments: a flooded section upstream of the main dam, a dewatered section between the dam and the main powerhouse, and a downstream section subject to powerhouse outflow. This chapter asks whether diversity and community composition

differ between the three future-impacted zones, with a particular focus on how these patterns affect conservation strategies for the region.

Understanding how taxonomic and functional community structure of fish assemblages in rapids change temporally between seasons, across major niche dimensions within seasons, and spatially along fluvial gradients will advance empirical knowledge of community assembly dynamics. By focusing these studies in the Xingu River, this knowledge can be further applied to conservation efforts by providing baseline data for monitoring programs and identifying key elements of community structure and dynamics that maintain diversity within this unique and highly threatened habitat.

CHAPTER II

SEASONAL CHANGES IN THE ASSEMBLY MECHANISMS STRUCTURING TROPICAL FISH COMMUNITIES

Overview

Despite growing interest in trait-based approaches to community assembly, little attention has been given to seasonal variation in trait distribution patterns. Mobile animals can rapidly mediate influences of environmental factors and species interactions through dispersal, suggesting that the relative importance of different assembly mechanisms can vary over short time scales. This study analyzes seasonal changes in functional trait distributions of tropical fishes in the Xingu River, a major tributary of the Amazon with large predictable temporal variation in hydrologic conditions and species density. Comparison of observed functional diversity revealed that species within wet-season assemblages were more functionally similar than those in dry-season assemblages. Further, species within wet-season assemblages were more similar than random expectations based on null model predictions. Higher functional richness within dry season communities is consistent with increased niche complementarity during the period when fish densities are highest and biotic interactions should be stronger; however, null model tests suggest that stochastic factors or a combination of assembly mechanisms influence dry-season assemblages. These results demonstrate that the relative influence of community assembly mechanisms can vary seasonally in response to changing abiotic conditions, and suggest that studies attempting to infer a single

dominant mechanism from functional patterns may overlook important aspects of the assembly process. During the prolonged flood pulse of the wet season, expanded habitat and lower densities of aquatic organisms likely reduce the influence of competition and predation. This temporal shift in the influence of different assembly mechanisms, rather than any single mechanism, may play a large role in maintaining the structure and diversity of tropical rivers and perhaps other dynamic and biodiverse systems.

Introduction

Community ecologists now recognize that multiple assembly mechanisms can operate simultaneously (Cavender-Bares et al. 2004, Spasojevic and Suding 2012) and have focused recently on how the relative influence of mechanisms change with spatial scale and spatial variation in environmental conditions. For example, environmental filtering (inferred from clustering of functional traits) appears to be the dominant mechanism structuring plant communities at the regional scale, whereas biotic interactions (inferred from dispersion of functional traits) have been shown to operate at finer scales (Weiher et al. 2011, Gotzenberger et al. 2012). Some studies of mobile animals have observed the opposite pattern, finding evidence for environmental filtering at small spatial grains and evidence of interspecific competition at larger grain sizes (Gotelli et al. 2010, Trisos et al. 2014). In temperate fish communities, environmental filtering was found to dominate across three spatial scales, though the types of traits driving functional similarity changed along a gradient of stream order (Troia and Gido 2015).

Considerably less attention has been given to how functional patterns and inferred assembly mechanisms vary temporally, despite wide recognition that ecological communities are highly influenced by temporal changes in environmental conditions (Junk et al. 1989, Walther et al. 2002, Houlahan et al. 2007). Most studies exploring temporal patterns of community assembly mechanisms analyze inter-annual changes. Purschke et al. (2013) found that the relative importance of environmental filtering in plant communities decreased throughout a 270-year successional chronosequence, in which different-aged patches were assumed to represent a temporal sequence of change. Through the use of permanent plots analyzed over 44 years, it was recently shown that decreases in phylogenetic and functional clustering in late successional stages result from colonization dynamics rather than the loss of closely related species (Li et al. 2015). In addition to variation in biotic factors, inter-annual fluctuations in precipitation rates have been shown to result in changes in the distribution of specific leaf area (Dwyer et al. 2014). Alternatively, inter-annual patterns of assembly of both plants and animals in experimental ponds changed very little over a 4-year period (Chase 2010). This focus on inter-annual changes in functional assembly partially reflects the large number of studies conducted on organisms with limited mobility over short time periods.

The mechanisms structuring the assembly of highly mobile animal species may vary over much finer temporal scales. Animals can rapidly mediate competitive interactions through dispersal, suggesting that even over short temporal scales unrelated to successional stage, assembly mechanisms can vary in response to ontogenetic shifts in dispersal abilities, seasonal migrations, or intra-annual changes in habitat availability.

For example, the phylogenetic dispersion and functional richness of euglossine bee communities have been shown to change seasonally in response to rainfall patterns (Ramirez et al. 2015). In tropical fish communities, temporal dynamics of colonization have been shown to change on the order of weeks, and vary according to stages of the hydrologic cycle (Arrington et al. 2005, Arrington and Winemiller 2006). On the other hand, tropical estuarine fish communities showed no clear temporal changes in trait distribution patterns, with environmental filtering appearing to dominate throughout the year (Mouchet et al. 2013). The magnitude and predictability of temporal environmental changes are known to influence the distribution of life history strategies in local assemblages, population stability, food web structure, and ecosystem productivity (Power et al. 2008, Sabo et al. 2010, Mims and Olden 2012, Jardine et al. 2015), and therefore should also affect community assembly dynamics.

Because they have large and predictable variation in hydrological discharge, tropical rivers are excellent model systems to illustrate the importance of considering temporal variation when inferring assembly mechanisms from functional diversity patterns. The ecology of large tropical rivers is strongly influenced by predictable hydrologic cycles and associated changes in available habitat and resources (Lowe-McConnell 1987, Junk et al. 1989, Chapman and Chapman 1993). During the annual flood pulse, increased volume and connectivity of aquatic habitat and high dispersal result in reduced densities of aquatic organisms relative to base-flow conditions during the dry season. These regular fluctuations in species density should strongly influence temporal patterns of biotic and abiotic factors affecting community structure, with biotic

interactions playing a greater role during low-water conditions (Arrington and Winemiller 2006). For example, the relative strength of top-down control of basal resources has been shown to shift with seasonal changes in hydrology, with stronger top-down effects during the low-water period (Winemiller et al. 2014).

To assess intra-annual changes in community assembly mechanisms, I investigated functional trait patterns of tropical fish communities in the lower Xingu River, Brazil, during dry and wet seasons. Specifically, I addressed two questions: 1) are wet-season assemblages more functionally similar than dry-season assemblages, and 2) are trait distributions of dry- and wet-season assemblages significantly different from patterns derived from random assembly. Due to increased potential for biotic interactions during the low-water period, trait distributions of dry-season assemblages should be relatively dispersed and more evenly spaced compared to wet-season assemblages. Previous studies of functional assembly of fishes have found a dominant pattern of trait underdispersion, suggesting that fish assemblages are generally structured by environmental filtering (Mason et al. 2007, Mouillot et al. 2007, Troia and Gido 2015); however, dry-season assemblages of perciform fishes in tropical and temperate rivers appear to be primarily structured by biotic interactions (Montaña et al. 2014). Therefore, temporal changes were expected to manifest as a shift from trait underdispersion during the wet season to random patterns during the dry season, with the latter resulting from stochastic colonization during the preceding falling-water period (Arrington et al. 2005) and/or the combined effects of abiotic and biotic filters canceling out (Swenson and Enquist 2009).

Metrics associated with single niche axes have been shown to have a higher power of detecting complex patterns of competition and habitat filtering (Trisos et al. 2014). I therefore separately examined two sets of traits related to different niche dimensions: habitat use and trophic strategy (Winemiller et al. 2015). Due to the selective pressure of high water velocities for convergence in body shape (Lamouroux et al. 2002, Lujan and Conway 2015) and prevalence of trophic niche partitioning in fishes of tropical rivers (*e.g.*, Lujan et al. 2012, Montaña et al. 2014), I hypothesized that fish assemblages would be underdispersed in traits related to habitat use, while traits related to trophic strategy would reveal overdispersion or even spacing.

Methods

Data Collection

Fish surveys were conducted along a 400-km stretch of the lower Xingu River, the largest clear water tributary to the Amazon River (Fig. 1A). This section of the river includes a 130-km complex of rapids and anastomosing channels over bedrock, known as the Volta Grande, which contains exceptionally high fish species richness and a variety of taxa specialized for life in high-velocity rapids (Fig. 1B). The hydrologic regime is strongly seasonal, with mean daily discharge recorded near the city of Altamira between 1976–2005 ranging from 1,222 m^3/s during the low-water period to 19,331 m^3/s during the high-water period (HidroWeb 2015). Water levels are lowest in September–October, when the river is composed of numerous shallow, braided channels with swift rocky rapids, and highest in March and April, when a 5-meter rise in water

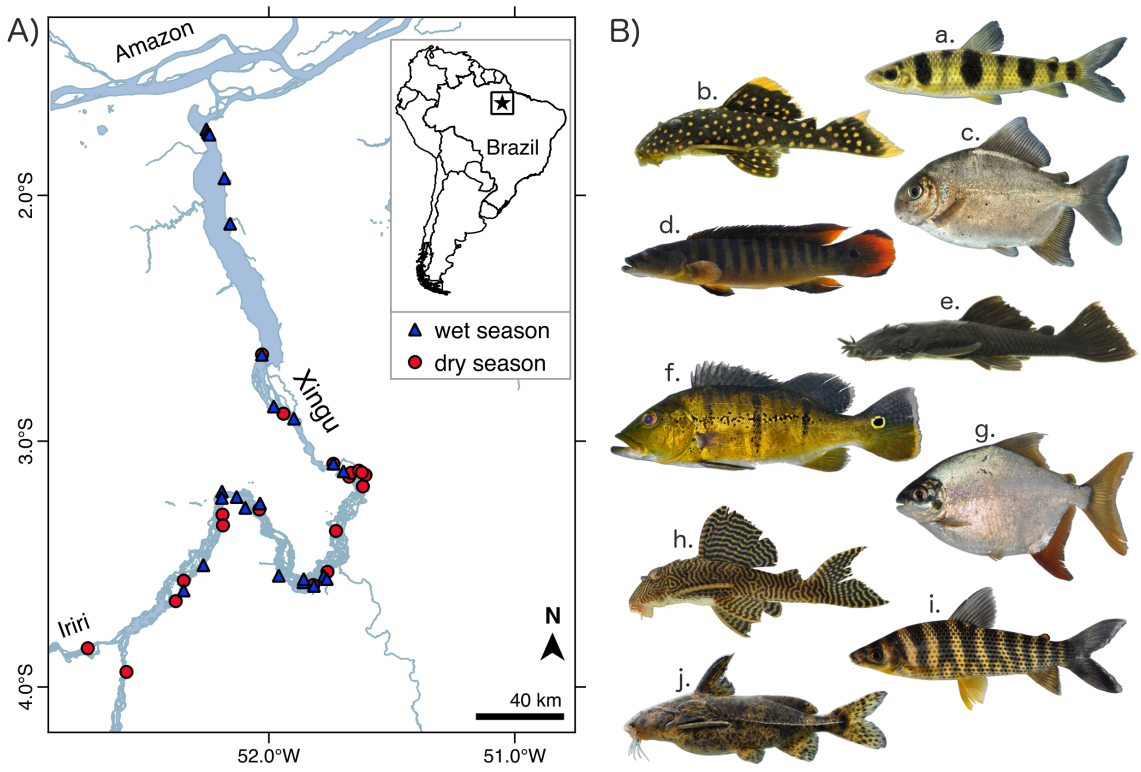

Figure 1. Study system, showing A) study site and sampling locations and B) several representative species. Each sampling location is a 100-m^2 reach and locations are separated by at least 1 km. Species shown are: a) *Leporinus maculatus* (Anostomidae), b) *Baryancistrus xanthellus* (Loricariidae), c) *Ossubtus xinguense* (Serrasalmidae), d) *Crenicichla sp.* (Cichlidae), e) *Ancistrus ranunculus* (Loricariidae), f) *Cichla melaniae* (Cichlidae), g) *Tometes kranponhah* (Serrasalmidae), h) *Hypancistrus sp.* (Loricariidae), i) *Leporinus tigrinus* (Anostomidae), and j) *Rhinodoras sp.* (Doradidae). Photos: Mark Sabaj Peréz

level forms a broad singular channel that inundates a relatively confined zone of riparian forest (Zuanon 1999, Sabaj Pérez 2015).

Fishes were collected by cast net and by hand while diving/snorkeling with the help of local fishermen, providing a unique opportunity for standardized sampling methods between dry- and wet-season main-channel habitats. Surveys targeted shallow rapids and deep, swift water over rocky substrates, with each sampling location

consisting of 60–80 minutes of fishing effort over an area of approximately 100 m^2. This technique primarily targets benthic species and those resident in rapids, though many highly mobile species were also sampled. A total of 148 species was collected from 20 sites during the 2013 dry season and 23 sites during the 2014 wet season (Fig. 1A). While attempts were made to sample the same locations in both seasons, the dangers of surveying rapids during high water required many sites be unpaired. Assemblage structure within major river sections was similar and variation in site placement should not bias seasonal analyses. In addition, β-diversity measured as Whittaker's β_w was similar between seasons (analysis of multivariate homogeneity of group dispersions; $F_{(1,41)} = 0.23$; $p = 0.64$), suggesting that spatial variation should not confound results.

Functional traits were measured for 41 of the most common rheophilous species, representing 9 families (*Appendix A*). Species pools varied slightly between seasons, resulting in 38 species accounting for 77% of abundance in dry season samples and 25 species accounting for 66% of abundance in wet season samples. Functional traits were divided into trait categories reflecting two primary niche dimensions following Winemiller et al. (2015). Nineteen morphological traits related to habitat use and swimming ability, such as body depth, fin dimensions, and eye position (hereafter 'Habitat') and 23 morphological traits related to feeding strategies, such as mouth width, gut length, and tooth shape (hereafter 'Trophic'), were measured on 3–6 adult individuals per species. Traits were selected for their clear relationships with habitat use and feeding ecology (Gatz 1979, Winemiller 1991); full descriptions of trait measurements are available in *Appendix B*. Length-based measurements were expressed

relative to standard length, body depth, or head length/depth as appropriate and averaged for each species (Winemiller 1991). Species mean trait values were log, n^{th} root, or inverse transformed to improve normality (see *Appendix B*), and Principal Components Analysis (PCA) was performed on standardized data for the combined species pools from both seasons to visualize niche trade offs within each trait category.

Data Analysis

To compare seasonal changes in functional community assembly, I first compared observed functional diversity between dry- and wet-season assemblages. Five functional diversity metrics were selected based on their power to distinguish assembly patterns (Mouchet et al. 2010, Aiba et al. 2013). Mean Nearest Neighbor distance (MNN) estimates how close species are in functional trait space, Standard Deviation Nearest Neighbor distance (SDNN) estimates how evenly species are spaced, Functional Richness (FRic) was measured as the convex hull and estimates overall niche volume, Functional Dispersion (FDis) was calculated as mean distance to centroid and estimates position relative to the center of niche space, and Functional Evenness (FEve) was measured as evenness of branches of a minimum spanning tree.

PCA was applied to the standardized data for habitat and trophic traits in each season separately. Species scores on the first two PC axes (explaining 63–66% of total morphological variation) were used to compute functional diversity measures based on species presence/absence per site in each season. FRic, FDis, and FEve were calculated using the package FD (Laliberté et al. 2014) and nearest neighbor distances were calculated using the fast nearest neighbor algorithm (Beygelzimer et al. 2013) in R

version 3.2.2 for OS X (R Core Team 2015). Observed functional diversity was only compared using the 21 species present in both seasons to control for variation in species richness; however, results were similar when all species were included. Functional diversity metrics for dry- and wet-season assemblages were compared using a Fligner-Killeen Test of Homogeneity of Variances and a Wilcoxon Rank Sum Test.

Functional diversity of local assemblages in each season was also compared to two null models based on species presence/absence, where the regional species pool was the 400 km stretch of river and local sites were 100 m^2 reaches. Both null models maintain observed species occurrence frequencies, but vary in how species richness among sites is treated. In the 'uniform-fixed' model, species randomly colonized local sites with equal probability so that richness per site varies, but each site has the same average richness (Gotelli 2000). The 'fixed-fixed' null model preserves observed differences in species richness between sites. By constraining both richness among sites and species occurrence frequency, the fixed-fixed model effectively tests for the impacts of species interactions and is widely used in community assembly studies. However, this model assumes nearly complete lists of species from well-defined habitat patches (*e.g.*, long-term censuses of islands), an assumption that is rarely met by short-term ecological censuses based on relatively standardized surveys. Gotelli (2000) argued that the uniform-fixed model might be more appropriate for short-term data. Therefore, I present results based on both null models for comparison. Simulations were run 1000 times and the five functional diversity metrics described above were calculated for each community. The fixed-fixed model used the matrix-swap algorithm of Gotelli (2000)

with a 1000 step burn-in and 500 step thinning parameter, implemented via the function RandomizeMatrix in the package picante (Kembel et al. 2010). Standard Effect Size (SES) was calculated as $(mean_{observed} - mean_{simulated})/ SD_{simulated}$ for each functional diversity metric, null model, and season. Significant dispersion from random assembly was assessed using a two-sided Wilcoxon Signed Rank Test of SES values. Results were compared qualitatively between seasons.

Results

The dominant pattern within functional niche space of fish assemblages from the lower Xingu River was the clear separation of species in the family Loricariidae from the remaining eight families in both the habitat and trophic dimensions (Fig. 2). The PCA of habitat traits (Fig. 2A) described a primary gradient (PC1) contrasting wide-bodied benthic species with large fins and eyes positioned high on the head against narrow-bodied species with relatively smaller fins and eyes positioned lower on the head. PC2 described a gradient from small, deep-bodied species to more elongate, shallow-bodied species that accounted for variation within the two major groups. Within the trophic dimension (Fig. 2B), PC1 described a gradient of species with long gut lengths, long gill rakers, and flat or rounded teeth typical of primary consumers and detritivores to species with shorter gut lengths, shorter gill rakers, and sharp-pointed teeth typical of carnivorous species. PC2 contrasted species with large oral gapes and numerous fine teeth with species having smaller mouths and fewer, more robust teeth. Species richness was highest for Loricariidae (20 spp.), which displayed a large amount

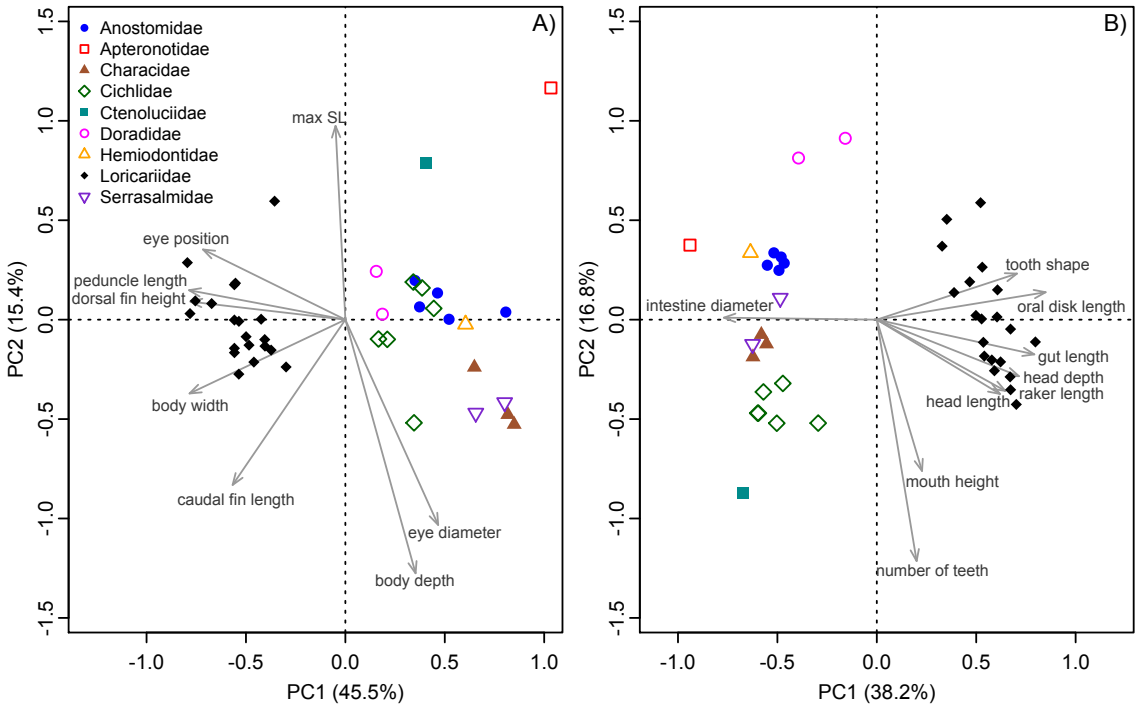

Figure 2. Principal Components Analysis (PCA) based on functional traits of combined species pools from local assemblages sampled during dry and wet seasons. PCA was run separately on standardized data for traits related to A) habitat use and B) trophic ecology. Only traits with the highest factor loadings on PC1 and PC2 are shown for clarity; a full list of traits used is provided as Supplemental Information.

of variation in both habitat and trophic niches compared to the other individual families. Several families, including Cichlidae, Anostomidae, and Characidae, revealed greater variation in habitat traits relative to trophic traits.

Observed functional diversity was significantly different between seasons, with similar temporal changes observed for both habitat and trophic traits (Fig. 3). Traits of wet-season assemblages were significantly clustered compared to dry-season communities based on MNN and FDis. In addition, FRic displayed significantly lower variance in wet-season assemblages. The evenness of trait distributions displayed a

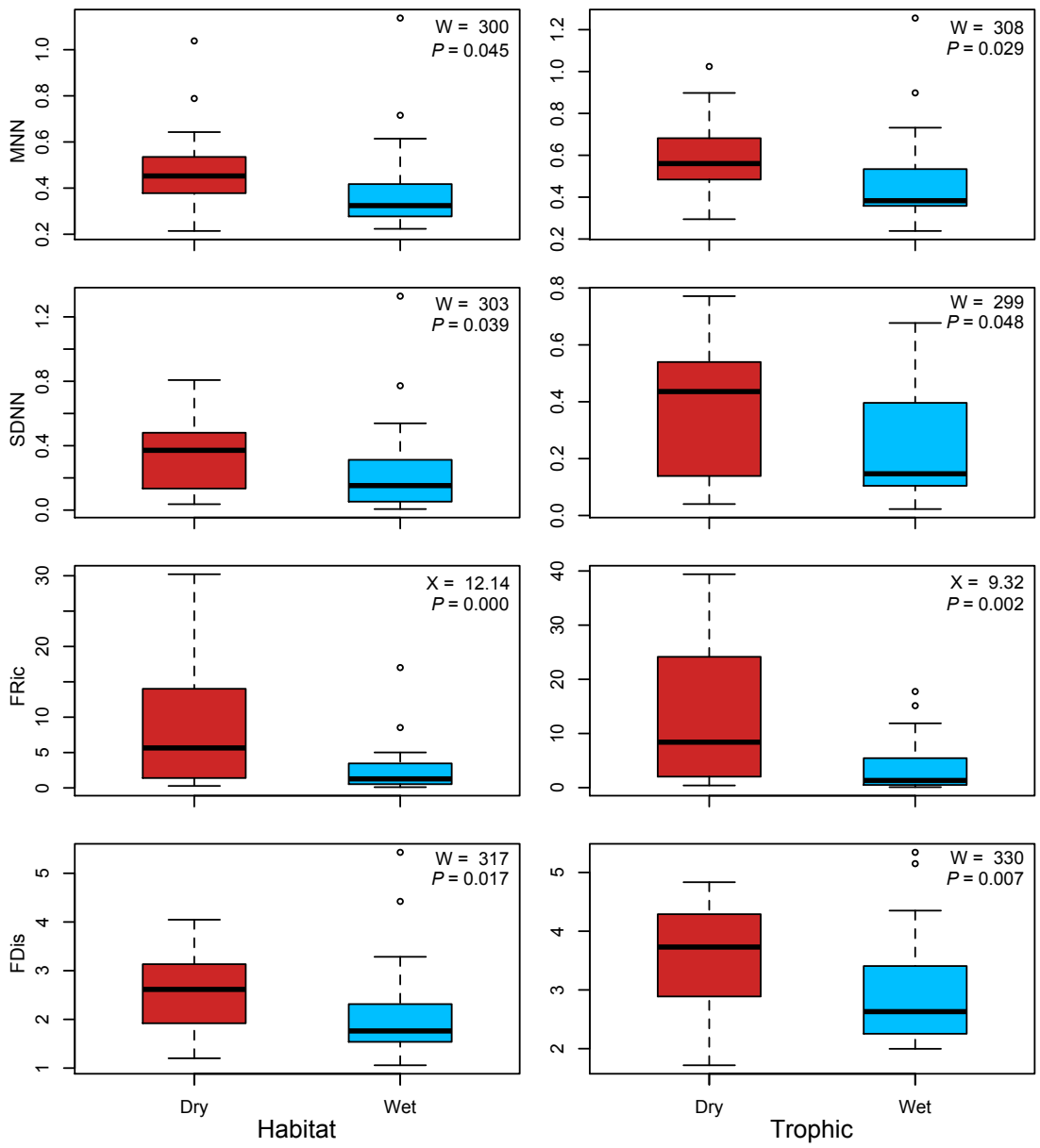

Figure 3. Comparison of observed functional diversity of local fish assemblages during dry and wet season based on traits related to habitat use (A) and trophic strategy (B). Functional diversity metrics refer to mean nearest neighbor distance (MNN), standard deviation of nearest neighbor distance (SDNN), functional richness as convex hull volume (FRic), and functional dispersion as mean distance to centroid (FDis). Functional evenness was not significantly different between seasons and is not shown here. Test statistics refer to Fligner-Kileen Test of Homogeneity of Variances (W) and Wilcoxon Rank Sum Test (X).

pattern opposite of that predicted, with wet-season samples being more evenly spaced (*i.e.*, lower SDNN) than dry-season samples. FEve was not significantly different between seasons (W = 174, $p = 0.089$; not shown in Fig. 3).

While results of null model comparisons differed slightly depending on the particular metric and null model used, wet-season assemblages tended to show more evidence of trait underdispersion than dry-season assemblages (Table 1). Dry- and wet-season assemblages both displayed strong evidence of being more tightly packed than random based on MNN, though results were marginally non-significant ($p = 0.056$) based on the fixed-fixed model for habitat traits in the wet season. However, only wet-season assemblages showed clear evidence of occupying a significantly smaller niche volume based on FRic. Wet season assemblages were significantly underdispersed in both habitat and trophic traits based on FRic for both null models, while only trophic FRic based on the uniform-fixed model revealed significant underdispersion in dry-season assemblages. Evidence for trait distributions being more evenly spaced than random was observed only for SDNN within the habitat dimension; however, the two null models differed in which season they detected significant underdispersion. FDis and FEve were not significantly different from random expectations for either niche dimension or null model. No evidence for trait overdispersion was found.

Discussion

Differences in functional diversity between wet- and dry-season fish assemblages support the hypothesis that the relative strengths of biotic and abiotic mechanisms of

Table 1. Results of two-sided Wilcoxon Signed Rank test of Standard Effect Sizes (SES) based on two null modeling approaches for each trait category. Median SES, test statistic, and p value are given. Significant results are presented in bold italics. Negative/positive SES values represent under/over dispersion of trait distribution compared to random expectation.

	Habitat		Trophic	
Diversity Index	uniform-fixed	fixed-fixed	uniform-fixed	fixed-fixed
Dry Season				
MNN	***–0.635*** ***V = 50*** ***p = 0.039***	***–0.586*** ***V = 48*** ***p = 0.032***	***–0.393*** ***V = 39*** ***p = 0.012***	***–0.180*** ***V = 42*** ***p = 0.017***
SDNN	***–0.560*** ***V = 51*** ***p = 0.044***	–0.553 V = 57 p = 0.076	0.085 V = 87 p = 0.522	0.096 V = 98 p = 0.812
FRic	–0.138 V = 95 p = 0.729	–0.482 V = 64 p = 0.133	***–0.363*** ***V = 13*** ***p = 0.000***	-0.215 V = 72 p = 0.230
FDis	0.097 V = 85 p = 0.475	–0.022 V = 83 p = 0.430	–0.328 V = 75 p = 0.277	–0.202 V = 84 p = 0.452
FEve	0.152 V = 130 p = 0.368	0.285 V = 131 p = 0.349	–0.046 V = 119 p = 0.622	–0.102 V = 102 p = 0.927
Wet Season				
MNN	***–0.440*** ***V = 56*** ***p = 0.011***	–0.529 V = 75 p = 0.056	***–0.576*** ***V = 63*** ***p = 0.021***	***–0.613*** ***V = 69*** ***p = 0.035***
SDNN	–0.476 V = 81 p = 0.086	***–0.495*** ***V = 70*** ***p = 0.039***	–0.663 V = 107 p = 0.360	–0.692 V = 99 p = 0.247
FRic	***–0.424*** ***V = 65*** ***p = 0.025***	***–0.376*** ***V = 72*** ***p = 0.045***	***–0.611*** ***V = 65*** ***p = 0.025***	***–0.440*** ***V = 30*** ***p = 0.000***
FDis	–0.371 V = 93 p = 0.179	–0.629 V = 92 p = 0.170	–0.472 V = 104 p = 0.314	–0.493 V = 92 p = 0.170
FEve	0.259 V = 181 p = 0.200	0.314 V = 183 p = 0.179	0.141 V = 168 p = 0.376	0.111 V = 157 p = 0.580

Notes: MNN = mean nearest neighbor distance, SDNN = standard deviation of nearest neighbor distance, FRic = functional richness measured as convex hull volume, FDis = functional dispersion measured as mean distance to centroid, and FEve = functional evenness measured as the evenness of branches of a minimum spanning tree.

community assembly can vary over the course of the annual hydrologic cycle. Direct comparison of functional diversity between seasons indicated that wet-season assemblages contained species that were more functionally similar than those in dry-season assemblages (Fig. 3). In addition, comparison with null models revealed that wet-season assemblages were significantly more similar than expected at random (Table 1), consistent with the idea that tropical fish assemblages in the wet season are highly structured by environmental filtering as they disperse and select habitats within expansive flooded areas. Higher values of MNN and FDis during the dry season suggest that local assemblages were composed of complimentary resource acquisition and habitat use strategies during a time when densities of aquatic organisms and, therefore, potential for competition were greatest. Null model results based on SDNN of habitat traits found some evidence consistent with an influence of limiting similarity during the dry season (Table 1). Wet-season assemblages also showed even spacing of habitat traits under the fixed-fixed model, though this should be interpreted with caution due to unmet model assumptions (see Methods).

In addition to evidence for limiting similarity, functional patterns observed in dry-season assemblages also suggest an increased influence of stochastic factors relative to wet-season assemblages. The increased variance in FRic during the dry season and non-significant null model results for most metrics are consistent with an influence of random colonization. Previous work on community assembly in tropical rivers has shown that initial patterns of patch colonization during the falling-water period are largely random, with increasingly deterministic patterns revealed over time (Arrington et

al. 2005). Stochastic colonization early in the dry season could lead to priority or mass effects, resulting in spatial variation in whether biotic or abiotic mechanism appears to dominate (Leibold et al. 2004, Allen et al. 2011). Results from experimental pond communities have demonstrated that increased productivity can lead to increased influence of stochastic processes and priority effects due to differential colonization (Chase 2010). Aquatic primary productivity is known to increase during dry season conditions in the main channel of clear-water tropical rivers (Cotner et al. 2006), suggesting that this same mechanism may also drive the increased stochastic patterns observed. Alternatively, the simultaneous influence of opposing assembly mechanisms can result in random patterns of trait dispersion even when the assembly process is highly deterministic (Weiher et al. 2011, Spasojevic and Suding 2012).

Higher variance of FRic and greater SDNN observed for dry season assemblages did not match predictions, but can be explained by seasonal turnover in the species pool and changes in occurrence frequencies. Specifically, higher variance in FRic was associated with a greater range in local species richness among dry-season samples (3–17 *spp*.) compared to wet-season samples (3–9 *spp*.). In addition, this turnover resulted in changes in the functional space occupied between seasons. While the majority of species in the family Loricariidae are present in collections from both seasons, several other families had more species with higher occurrence frequencies in dry-season samples, with the families Anostomidae and Serrasalmidae only present in dry-season collections. The Loricariidae occupy a distinct region of morphological trait space (Fig. 2), resulting in two distinct functional groups inhabiting Xingu rapids. The higher

number of species occupying the non-loricariid functional group within local assemblages during the dry season yielded greater variance in trait spacing.

Differences in statistical results from the two null models may also be explained by seasonal shifts in functional spaces occupied within local assemblages. Because the uniform-fixed model effectively compares observed assemblages against a simulated average, it was more sensitive to additional species occupying the periphery of local assemblage morphological space during the dry season. SES SDNN was a particularly sensitive metric, with the two null models revealing opposite seasonal patterns for habitat-associated traits. Given the short duration of each survey and unpaired design, the uniform-fixed model should provide a more appropriate test of these data (Gotelli 2000), and would further support predictions for SDNN. While this model does not control for variation between sites, similarity of habitat and assemblage structure (β_w) across sites suggest that changes reflect real temporal differences in the average assemblage. These differences highlight the importance of carefully selecting functional traits, associated diversity metrics, and null models for statistical inference. Explicitly discussing model assumptions and potential data limitations may aid interpretation of results, as well as comparisons across studies.

Because the current study focused on main-channel habitats, seasonal turnover in the species pool was likely influenced by interspecific differences in lateral migrations into floodplain habitats during the high-water period. Although some loricariids have local dispersal associated with ontogeny, lateral migrations onto floodplains are rare (Fernandes 1997, Lucas and Baras 2001). Indeed, 17 species of loricariids (out of 19

analyzed) were captured during both seasons, suggesting that many of these species are highly sedentary in rocky habitats within the main channel. The absence of two species of the family Serrasalmidae (*Ossubtus xinguense* and *Tometes kranponhah*) from wet-season samples is consistent with the migratory behavior of related species known to use flooded forests as feeding and nursery grounds during the high-water period (Lucas and Baras 2001, Correa et al. 2007). Similarly, the absence of Anostomid species from wet season samples is consistent with seasonal movements described for these fishes (Fernandes 1997, Lucas and Baras 2001, Makrakis et al. 2012). Differences in sampling efficiency between seasons also could have influenced patterns of species turnover. High turbidity during the wet season reduces visibility, which could have affected divers' ability to capture fishes swimming within the water column. Many of the species found in the water column of high velocity rapids (*e.g.*, anostomids) were captured with cast nets, which are less efficient during the high-water period. Nonetheless, analyses performed using only species of Loricariidae, which have a consistent sampling efficiency as evidenced by low seasonal turnover, produced identical temporal patterns in trait distributions. This suggests that seasonal changes reflect real differences in the strength of assembly mechanisms rather than sampling bias.

Despite strong selection for convergent body morphology in rapids-dwelling species, Xingu fishes have slight differences that allow species to exploit structurally complex and heterogeneous microhabitats within rocky substrates. The even spacing of habitat traits and underdispersion of trophic traits reflect adaptations to exploit similar resources in a variety of microhabitats. Although PCA revealed large variation in trophic

traits, species existing on the periphery of this space were relatively rare and had little influence on functional diversity patterns. Species with the highest occurrence frequencies (*e.g.*, *Baryancistrus xanthellus, Spectracanthicus punctatissimus, S. zuanoni, Ancistrus ranunculus*) all have similar jaw and gut morphologies that facilitate feeding on benthic algae and detritus. However, these same species display large variation in body depth, with strongly dorso-ventrally compressed species, such as *A. ranunculus*, able to occupy narrow spaces between rocks that deeper-bodied species cannot access (Fig. 1B). Whereas previous studies have hypothesized that periphyton grazers and detritivores may partition trophic niches based on stoichiometric differences (Hall 2004, Lujan et al. 2012), my results imply that microhabitat partitioning is more influential in facilitating coexistence of diverse benthivorous fishes in the Xingu River. Large interspecific variation in body shape associated with habitat use is also displayed among fishes occupying other trophic positions. For example, insectivorous and carnivorous species of the family Cichlidae vary greatly in relative body depth (Fig. 1B), a trait that strongly influences performance in relation to flow velocity and substrate complexity.

While structural complexity should facilitate species co-occurrence at the local scale, seasonal relaxation of competition and predation within expanded aquatic habitat during the high-water period may play a major role in maintaining high fish diversity over a larger scale. Increased inputs of terrestrial resources during the wet season together with decreased species density should enhance fitness via greater surplus energy for growth, reproduction, and migration. It has been suggested that the predictable, gradual increase in water level during the annual flood pulse of tropical rivers should

result in competitive release among fishes (Junk et al. 1989), a hypothesis consistent with findings from this study and others (e.g., Correa and Winemiller 2014). These results stress the importance of evaluating temporal changes in functional patterns when attempting to infer assembly mechanisms. Data collected over a restricted time period would be unlikely to shed light on the interplay of multiple factors influencing communities of rivers and other dynamic ecosystems.

The degree of predictability and magnitude of environmental change will affect the relevant temporal scale, as well as our ability to infer mechanisms from patterns. Communities experiencing high magnitude changes (*i.e.*, stress inducing) may display little temporal variation in assembly mechanisms after environmental change. For example, experimentally induced drought in pond mesocosms increased the influence of environmental filtering for two years after the perturbation (Chase 2007). Shallow floodplain depressions that experience hypoxic conditions during the dry season show little inter-annual variation in fish species composition, despite high colonization potential during the annual flood period (Chapman and Chapman 1993). In communities experiencing unpredictable environmental fluctuations, such as the flashy hydrologic regimes of high gradient streams, assembly mechanisms may fluctuate so rapidly that dynamics appear largely stochastic throughout the year. Additionally, temporal variation may remain highly dependent on spatial scale, and studies integrating both temporal and spatial variation in functional trait patterns are needed to explore this potential interaction.

Several authors have cast doubt on the assumption that functional trait clustering reflects environmental filters and trait dispersion indicates a strong influence from biotic interactions (HilleRisLambers et al. 2012, Herben and Goldberg 2014). Indeed, many fishes use floodplain habitats for both resource acquisition and refuge from predation (Winemiller and Jepsen 1998). Therefore, the significant underdispersion observed in wet-season assemblages could arise not only from habitat filtering based on resource availability, but also spatial variation in predation vulnerability. This emphasizes the need to consider temporal dynamics when attempting to infer assembly processes. While trait distributions in either season could reflect multiple assembly mechanisms, the greater interspecific trait similarity observed in wet-season assemblages is consistent with predictions based on seasonal changes in species density and resource availability.

While many studies have used functional traits to infer the dominant mechanisms structuring communities, few have considered the strong potential for mechanisms, and therefore functional patterns, to change seasonally. Using tropical fishes inhabiting rapids as a model, I demonstrated that functional assemblage structure varies between hydrologic seasons. This variation reveals the interplay of multiple assembly mechanisms and suggests that studies analyzing functional patterns from a single season may overlook key aspects of the assembly process. Temporally shifting influences of multiple assembly mechanisms, rather than any specific mechanism, may play a large role in structuring high diversity systems, such as tropical rivers.

CHAPTER III

USING TROPHIC STRUCTURE TO REVEAL PATTERNS OF TRAIT-BASED COMMUNITY ASSEMBLY ACROSS NICHE DIMENSIONS

Overview

Trait-based approaches to community assembly are limited by the potential for multiple deterministic assembly processes to operate along different niche axes simultaneously. Analyzing individual traits may aid understanding of assembly processes; however, single traits may influence multiple niche dimensions, complicating this approach. This study used correlations between functional traits and stable isotope ratios to objectively associate traits with trophic niches, and then tested for a relationship between these associations and how the distributions of traits within local assemblages deviate from expectations under random assembly. Specifically, I tested whether traits with higher correlations to trophic structure display increased deviation from null expectations within tropical fish communities. A significant relationship was found between a trait's deviation from null expectations and its correlation with isotopic patterns, with traits strongly associated with trophic structure displaying greater dispersion from the mean and more evenly spaced trait values than weakly associated traits. Traits strongly associated with trophic structure were also more clustered, a possible reflection of trophic niche diversification around adaptive peaks. These results suggest that traits strongly associated with trophic ecology are more influential in niche differentiation affecting species coexistence compared to weakly associated traits, and

demonstrate that certain traits may respond to assembly mechanisms in predictable ways despite the complex, multidimensional nature of the assembly process.

Introduction

Trait-based approaches offer a path towards increased generality and predictability for community ecology (McGill et al. 2006), with a growing body of literature inferring community assembly mechanisms from functional diversity patterns (Weiher et al. 2011, Gotzenberger et al. 2012). Comparing observed functional diversity of co-occurring species to that expected under random assembly provides a test of whether trait-equalizing processes (*e.g.*, environmental filtering, competitive hierarchies) or niche-stabilizing processes (*e.g.*, limiting similarity) drive community assembly; however, this approach is limited by the potential for multiple deterministic assembly processes to operate simultaneously within an assemblage (Weiher et al. 1998, Cavender-Bares et al. 2004, Grime 2006, Kraft et al. 2008, Ingram and Shurin 2009, Swenson and Enquist 2009). In addition, it is becoming increasingly clear that similar distributions of functional traits within local assemblages may result from different mechanisms of community assembly (HilleRisLambers et al. 2012, Herben and Goldberg 2014, Kraft et al. 2014), making patterns of multivariate functional diversity difficult to interpret.

Recent theoretical and empirical studies have emphasized the need to evaluate specific traits or groups of traits related to specific functions in order to fully understand how trait distributions within communities reflect underlying assembly mechanisms

(Spasojevic and Suding 2012, Laughlin 2014, Trisos et al. 2014, Troia and Gido 2015, Winemiller et al. 2015). Niches have multiple dimensions, and functional diversity may deviate from random expectations in predictable ways depending on the traits analyzed. The degree of consistency in trait response to a given mechanism will ultimately determine the predictive power of the trait-based approach; yet, few studies have sought means to test for general patterns (Ackerly and Cornwell 2007, Ingram and Shurin 2009, Herben and Goldberg 2014).

The expected distribution of a given trait within a local assemblage will depend on the relative strength of abiotic and biotic pressures, as well as rates of productivity, disturbance, and dispersal (Grime 2006, Chase and Myers 2011). In environmentally stressful conditions, traits highly correlated with habitat characteristics should be clustered in community trait space due to environmental filtering. For example, the presence of fish with special respiration adaptations in hypoxic floodplain pools (Chapman and Chapman 1993) or plants with short stature and low leaf area in wind-exposed alpine environments (Spasojevic and Suding 2012) both reflect filtering of traits in response to stressful conditions. If habitat is spatially heterogeneous over the scale of study or space is limiting, traits associated with habitat features may be more functionally diverse than expected at random due to niche-stabilizing mechanisms of assembly (*e.g.*, limiting similarity). Difference in body shape/size between fishes inhabiting riffles or pools (Lamouroux et al. 2002, Troia and Gido 2015) and differences in limb and body size of ground-dwelling or arboreal *Anolis* lizards (Losos 2009) provide two examples of trait variation associated with habitat partitioning. Limited food

resources may cause traits that are strongly associated with resource acquisition to be more functionally diverse than expected at random. For example, Neotropical fishes (Lujan et al. 2012) and birds (Trisos et al. 2014) show large variation in mouth and beak morphology that likely reflect niche partitioning through alternative foraging strategies. Determining the conditions under which certain traits are most likely to respond to a given mechanism will be a critical step in developing a general theory of community assembly.

Progress towards understanding differential response of traits across niche axes will require novel approaches to test hypotheses about the expected distribution of trait values within local assemblages and how these compare to distributions under random assembly processes. Although pioneering work on ecomorphology of fishes used stomach contents analysis to inform trait-based approaches (Gatz 1979) and several authors have explored relationships between stable isotope signatures of consumers and their functional traits (Lujan et al. 2011, Domínguez et al. 2012, Gibb et al. 2015, Pool et al. 2016), few studies have used consumer isotopic signatures to interpret or predict how trait distributions within local assemblages compare to random expectations. Stable isotope signatures of consumers and food resources can be used to estimate consumer resource assimilation (Peterson and Fry 1987, Phillips et al. 2014), and relative positions in isotope bi-plot space can serve as proxies for relative positions in community trophic space (Layman et al. 2007). Correlations between functional traits and isotopic signatures, combined with detailed knowledge of trait functions, may aid in determining a trait's association with trophic ecology and provide a basis for testing predictions of

differential trait response. For example, Ingram and Shurin (2009) used stable isotope ratios of nitrogen to show that traits related to trophic position in Pacific rockfishes have more evenly spaced values than expected at random, suggesting competition for resources has led to niche segregation in these assemblages. Similar approaches could provide insight into the complex patterns that occur when assembly mechanisms promoting functional divergence interact with those promoting functional clustering, resulting in highly deterministic processes that produce community patterns indistinguishable from random assembly (Spasojevic and Suding 2012). If traits associated with resource acquisition consistently respond to mechanisms promoting functional divergence (*e.g.*, limiting similarity), the distributions of individual traits within local assemblages should reflect this regardless of the significance of overall community patterns (*i.e.*, patterns derived from multiple traits having diverse functions).

This study explores the relationship between trophic structure and the distributions of functional traits within assemblages of rapids-adapted fishes in the Xingu River, a major Amazon tributary. Studies in a wide range of stream and riverine habitats have found evidence of trophic niche partitioning in fishes (Gatz 1981, Ross 1986, Lujan et al. 2012, Montaña et al. 2014), and there is strong evidence of convergence in the morphology of rheophilic fishes globally (Lamouroux et al. 2002, Lujan and Conway 2015). This suggests that fish communities in rapids may experience strong pressure from opposing assembly processes, wherein traits involved in swimming and habitat use tend to converge and feeding traits show divergent patterns (Gatz 1981, Ackerly and Cornwell 2007, Ingram and Shurin 2009). Specifically, I test whether traits

that have stronger correlations with stable isotope signatures display greater dispersion relative to a null model of community assembly. I further explore how well stable isotope ratios predict functional diversity patterns and whether *a priori* groupings of traits according to functions related to trophic strategy or habitat use differ in their associations with isotopic patterns.

Methods

Data Collection

Analyses were based on fish surveys conducted during the 2013 dry season along a 400-km stretch of the Xingu River, the largest clear-water tributary to the Amazon River. This section of the river includes a 130-km complex of rapids and anastomosing channels over bedrock, known as the Volta Grande, which contains exceptionally high diversity and species well adapted for life in swift water. Fishes were collected by cast net and by hand while diving/snorkeling with the help of local fishermen. Ninety-two species were collected from 20 sites, each of which was surveyed with 60–80 minutes of fishing effort over an area of approximately 100 m^2 encompassing shallow rapids and deep, swift-flowing channels over rocky substrates. Dry-season survey data were selected for analyses because previous work revealed both functional clustering and functional divergence within these communities depending on the metric used, suggesting the potential for different traits to be responding to different assembly mechanisms (see Chapter II).

Functional traits were measured for 37 of the most abundant rheophilic species in my samples for which isotopic data were also available (*Appendix C*). These species represent 9 families and accounted for 72% of the total fish specimens captured. Due to insufficient sample sizes for species in the genus *Crenicichla*, and their high interspecific morphological and isotopic similarity, one nominal and three un-described species were pooled together (*Crenicichla* spp.) for the purpose of this analysis. Traits were divided *a priori* into two niche dimensions based on their clear functional role in habitat use and feeding ecology (Gatz 1979, Winemiller 1991, Winemiller et al. 2015). Nineteen body and fin measurements that influence swimming performance and habitat use comprised the 'Habitat' category. Twenty-six traits that influence feeding performance, such as mouth width, gut length, and tooth shape comprised the 'Trophic' category. Measurements were made on 3–6 adult individuals per species; a full list of traits and descriptions of measurements are available in *Appendix B*. Length-based measurements were expressed relative to standard length, body depth, or head length/depth as appropriate and averaged for each species (Winemiller 1991). Species mean trait values were log, n^{th} root, or inverse transformed to improve normality, and were standardized prior to analysis.

Samples used for isotopic analysis were collected from muscle tissue of 3–7 adult individuals per species (with the exception of *Sternarchorynchus sp.* for which only two samples were available). In most cases, these were the same individuals used for functional trait measurements. Samples were prepared following standard protocols (Arrington and Winemiller 2002) and analyzed at the Center for Applied Isotope

Studies' Stable Isotope Ecology Laboratory at the University of Georgia, Athens. Ratios of heavy to light isotopes of C and N were expressed relative to standards (Pee Dee Belemnite and atmospheric N_2, respectively) and reported in delta notation ($\delta^{13}C$ and $\delta^{15}N$). $\delta^{13}C$ and $\delta^{15}N$ values were used as estimates of relative position in trophic space. Because samples were collected from similar habitats within the same region during the dry season, spatial and temporal variation in isotopic signatures should not bias estimates. Samples for each species were taken from multiple sites throughout the study reach and average values per species were used for all analyses. Because variation in lipid content between species can impact analysis of C isotope ratios, $\delta^{13}C$ values were corrected using the equation: $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N$ (Post et al. 2007). In addition, benthic algae are the dominant production source supporting most fishes in this river during the dry season (Zuluaga Gómez et al. 2016), so that variation in vertical positions of consumers in isotopic space due to assimilation of alternative sources with different $\delta^{15}N$ should be minimal.

Data Analysis

Observed assemblage data were first compared to a null model based on species presence/absence within sites, where the regional species pool was the 400 km stretch of river and local sites were 100 m^2 reaches. The null model maintained observed species occurrence frequencies, as well as observed differences in species richness between sites. Randomizations followed the matrix-swap algorithm of Gotelli (2000) with a 1000 step burn-in and 500 step thinning parameter, implemented via the function RandomizeMatrix in the package picante (Kembel et al. 2010) using R version 3.2.2 for

OS X (R Core Team 2015). Simulations were run 1000 times and functional diversity metrics were calculated for each trait based on Euclidean distances between standardized trait values of species present within each site. Five functional diversity metrics were selected based on their power to distinguish assembly patterns (Aiba et al. 2013): *range* estimates overall diversity of trait values present, *variance* estimates trait dispersion relative to the mean (*i.e.*, center of functional space), *Mean Nearest Neighbor Distance (MNND)* estimates how close trait values are in functional space, *Standard Deviation Nearest Neighbor Distance (SDNND)* estimates how evenly trait values are spaced, and *SDNND/range (SDNNDr)* estimates how evenly trait values are spaced relative to the diversity of trait values present.

Standard Effect Size (SES) of each functional diversity metric was calculated as $(\text{observed} - \text{mean}_{\text{simulated}}) / \text{SD}_{\text{simulated}}$ for each trait within each site. SES measures how different the distribution of a trait within a local assemblage is from random expectation, with a positive SES value for *range*, *variance*, and *MNND* indicating that the fish assemblage at that site has higher functional diversity than expected by chance for that trait. For *SDNND* and *SDNNDr*, a positive SES indicates that the fish assemblage at a given site is more unevenly distributed in functional space than expected by chance. Because SES reflects both the magnitude and direction of deterministic assembly processes, and facilitates comparison across studies, these values were used as a response variable in subsequent analyses.

A linear modeling approach was then used to test for a relationship between a trait's divergence from random expectations (SES values) and a trait's correlation to

trophic position. Spearman rank correlations were calculated between each trait and each isotopic element based on average values per species. These correlations provide a continuous measure of a trait's association to trophic position ($\delta^{15}N$ and $\delta^{13}C$) and differ from the *a priori* categorization described above, in which the Trophic category reflects both trophic position and differences in foraging behavior. Linear mixed effects models were used to control for the inherent correlations between functional diversity measures of different traits within the same local assemblage. SES values calculated from the null model were included as response variables. The absolute value of spearman rank correlations of each trait with $\delta^{15}N$ and $\delta^{13}C$ were considered fixed effects and site was included as a random intercept. Models were fit by restricted maximum likelihood using the package lme4 and parametric bootstrapped confidence intervals were used to assess significance of fixed effects (Bates et al. 2015). Constrained and marginal R^2 values were calculated following Nakagawa and Schielzeth (2013) using the function sem.model.fits in the package piecewiseSEM (Lefcheck 2015).

To explore relationships between functional patterns, isotope ratios, and trait categories, I first used redundancy analysis (RDA) of standardized traits on standardized $\delta^{15}N$ and $\delta^{13}C$ values to test whether isotopic signatures explain a significant amount of the morphological variation present in the species pool. RDA was performed using the function rda in the package vegan (Oksanen et al. 2015). Tests of significance of RDA and explanatory variables were performed by permutation; tests of explanatory variables followed the marginal method of (Legendre et al. 2011). Constrained and residual ordinations were used to visualize niche tradeoffs between species. Finally, t-tests were

used to test whether mean correlations with $\delta^{15}N$ and $\delta^{13}C$ differed between trait categories and box plots were used to visualize the distribution of correlations across categories.

Results

A significant relationship was found between a trait's deviation from null expectations (*i.e.*, SES values) and its correlation to isotope values, although results differed slightly between functional diversity metrics and isotopic elements (Fig. 4 and Table 2). Traits with higher correlation with $\delta^{15}N$ tended to have values further from the mean, more clustered together, and more evenly spaced within local assemblages, whereas traits with higher correlation with $\delta^{13}C$ tended to be more clustered and more evenly spaced. SES variance was positively related to trait correlation with $\delta^{15}N$, indicating that a trait's average distance from the mean is relatively greater with increasing correlation to vertical trophic position. SES variance showed no relationship with trait correlation with $\delta^{13}C$. SES MNND was negatively related to trait correlations with both $\delta^{15}N$ and $\delta^{13}C$. Contrary to my predictions, it appears traits are more clustered within functional space as correlation with trophic position increases. At the same time, traits become more evenly spaced with increasing correlation to trophic position. SES values of both SDNND and SDNNDr displayed a negative relationship (*i.e.*, increasingly even) with trait correlations with $\delta^{15}N$. SES range showed no relationship with trait correlations with $\delta^{15}N$ or $\delta^{13}C$. Marginal R^2 values were consistently lower than

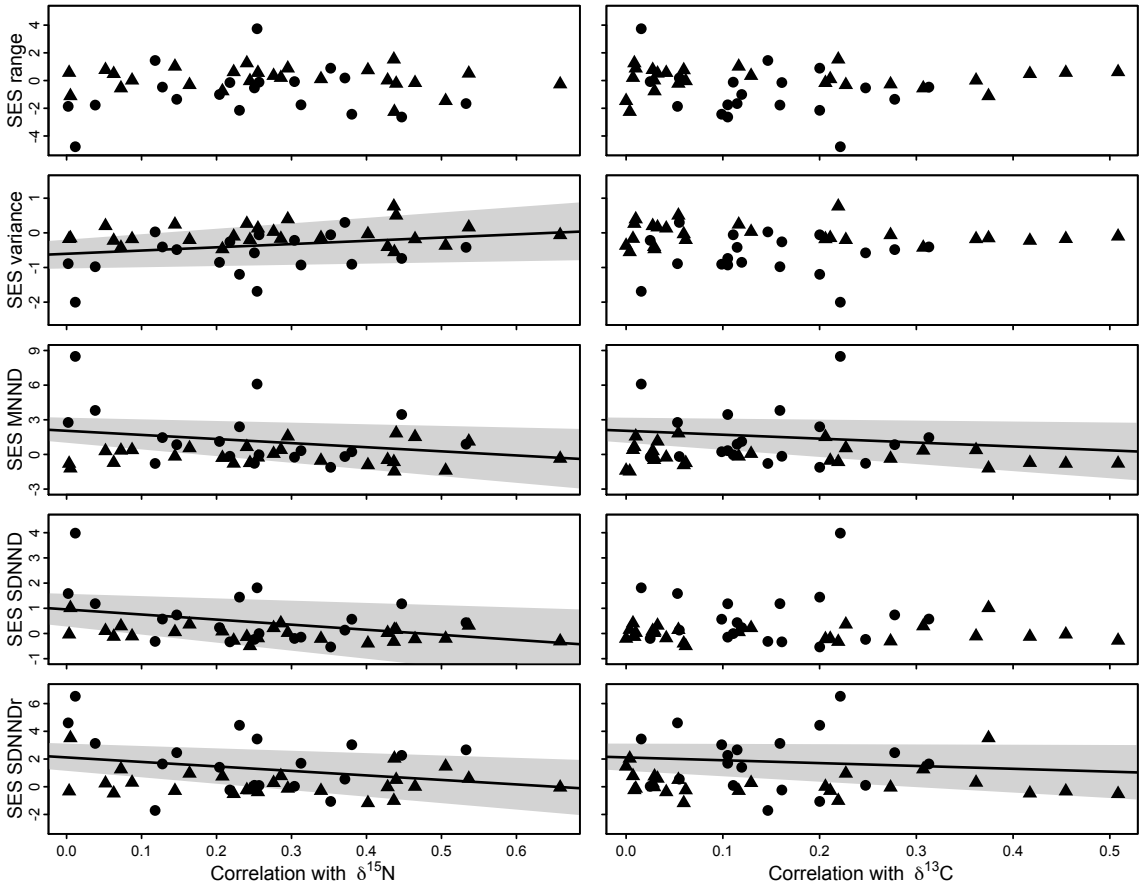

Figure 4. Relationship between Standard Effect Size (SES) and spearman rank correlation with isotopic ratios of N (δ^{15}N, left panel) and C (δ^{13}C, right panel) for 45 morphological traits. Points represent mean SES values across 20 sites and are coded by trait category: Habitat (circles) and Trophic (triangles). Black lines show mean trend for significant fixed effects of δ^{15}N and δ^{13}C based on linear mixed effects models with site included as a random intercept. Gray shaded regions represent 95% confidence intervals based on parametric bootstrapping. Abbreviations are for Mean Nearest Neighbor Distance (MNND), Standard Deviation of Nearest Neighbor Distance (SDNND), and SDNND/range (SDNNDr).

conditional R^2 (Table 2), demonstrating that fixed effects accounted for a small portion of the variance explained by each model

Isotopic signatures explained a significant portion of the functional variation present in the species pool based on the full RDA model (F = 2.19, *P* = 0.02; Fig. 5).

Table 2. Results of linear mixed effects models for standard effect size of functional diversity measures. Models fit by restricted maximum likelihood with $\delta^{13}C$ and $\delta^{15}N$ as fixed effects and site as a random intercept. Bold text indicates significant fixed effects based on parametric bootstrapped 95% confidence intervals (CI). Marginal ($_M$) and conditional ($_C$) R^2 values calculated following Nakagawa and Schielzeth (2013).

	$\delta^{15}N$		$\delta^{13}C$			
Response	Estimate (SE)	95% CI	Estimate (SE)	95% CI	R^2_M	R^2_C
range	0.34 (1.15)	(–1.87, 2.68)	–0.29 (1.42)	(–3.14, 2.37)	0.00	0.06
variance	**0.94 (0.31)**	**(0.32, 1.54)**	0.36 (0.39)	(–0.44, 1.15)	0.01	0.23
MNND	**–3.56 (1.11)**	**(–5.69, –1.37)**	**–3.39 (1.37)**	**(–6.13, –0.68)**	0.01	0.07
SDNND	**–2.01 (0.60)**	**(–3.14, –0.87)**	–0.98 (0.74)	(–2.50, 0.45)	0.01	0.11
SDNNDr	**–3.25 (0.77)**	**(–4.64, –1.71)**	**–2.05 (0.95)**	**(–3.86, –0.18)**	0.02	0.24

Notes: MNND = mean nearest neighbor distance, SDNND = standard deviation of nearest neighbor distance. SDNNDr = standard deviation of nearest neighbor distance/range

Further tests of explanatory variables found a significant effect of $\delta^{15}N$ ($F = 3.56$, $P = 0.01$) and no effect of $\delta^{13}C$ ($F = 0.81$, $P = 0.56$). RDA1 was largely influenced by $\delta^{15}N$, whereas $\delta^{13}C$ was strongly correlated with RDA2. Variation along RDA1 was mainly associated with traits in the Trophic category, such as gut length, snout length, mouth position, and oral disk width. Body width (which influences stability and turning ability) also loaded heavily on RDA1. The portion of variation explained by isotopic signatures was low (adjusted $R^2 = 0.062$), with RDA1 and RDA2 explaining only 11.6% of total variation (Fig. 5). A large amount of residual variation remained in the first two principal component axes (Fig. 5B), with clearly interpretable functional groupings based largely on traits related to habitat use and swimming ability.

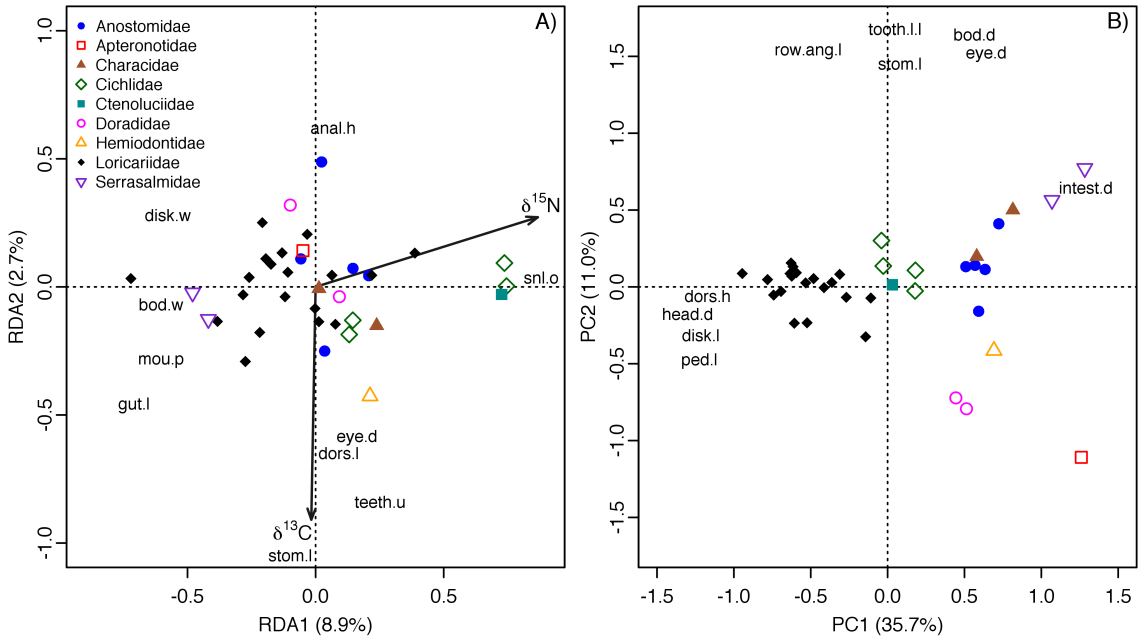

Figure 5. Redundancy analysis of standardized morphological traits on standardized isotope ratios ($\delta^{15}N$ and $\delta^{13}C$). Points are mean values for each species and symbols represent different families. Only traits with the 10 highest factor loadings are presented for clarity; trait abbreviations represent the apices of vectors originating from the origin. Arrows represent explanatory variables. Panel A) shows results of the constrained analysis plotted using the matrix of fitted values projected on the explanatory variables $\delta^{15}N$ and $\delta^{13}C$. Panel B) shows residual variation not accounted for by the RDA model. Trait abbreviations and descriptions are provided in Table S2 in Supporting Information.

There was no significant difference between trait categories based on comparisons of mean trait correlation with $\delta^{15}N$ ($mean_{Habitat} = 0.240$, $mean_{Trophic} = 0.280$, $t = –0.82$, $P = 0.21$) or $\delta^{13}C$ ($mean_{Habitat} = 0.142$, $mean_{Trophic} = 0.160$, $t = –0.49$, $P = 0.31$). While many of the highest correlations with $\delta^{15}N$ and $\delta^{13}C$ were for traits related to feeding (*e.g.*, gut length, snout length, mouth width, tooth shape), not all traits in the Trophic category were highly correlated with isotopic values (Fig. 6). Some traits in the Habitat category also displayed high correlation with trophic position (*e.g.*, body width, caudal peduncle

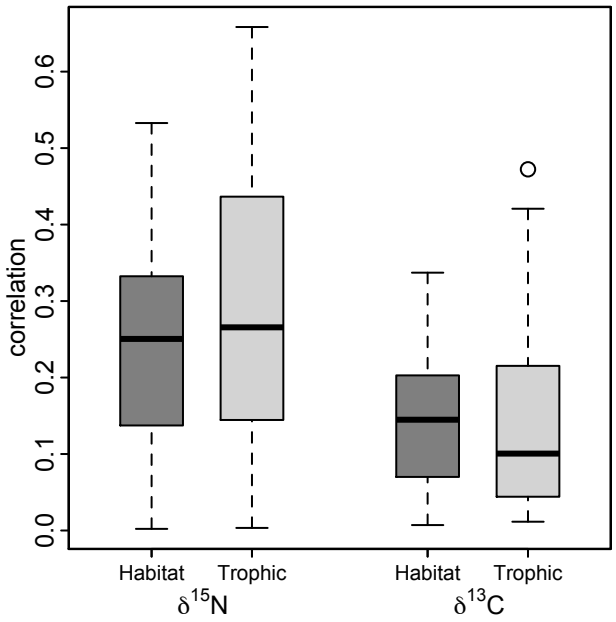

Figure 6. Distributions of absolute value of spearman rank correlations between 45 morphological traits and isotopic ratios ($\delta^{15}N$ and $\delta^{13}C$) by trait category (Habitat and Trophic). For each element, mean values between categories are not significantly different based on a t-test.

length, and anal fin length). In general, trait correlations with $\delta^{15}N$ tended to be higher than those with $\delta^{13}C$.

Discussion

Support was found for the prediction that traits with higher correlation with trophic position tend to be more functionally diverse and evenly distributed in functional space relative to other traits within local assemblages. The positive relationship found for SES variance and negative relationships found for SES of SDNND and SDNNDr (Fig. 4) suggest that traits associated with trophic position are tending to diverge within

local assemblages relative to other traits and may be responding more to mechanisms promoting stabilizing niche differences (*e.g.,* limiting similarity). The higher values found for conditional R^2 relative to marginal R^2 (Table 2) indicate that species identity within local assemblages strongly impacts these relationships, with the presence/absence of functionally distinct species (*e.g.*, the knife fish *Sternarchorhynchus sp.* Apteronotidae) disproportionately affecting differences between sites. The negative relationship found for SES MNND did not match predictions, revealing that traits associated with trophic position also tend to be more clustered around specific values compared to other traits. These results suggest that while species within local assemblages tend to segregate niches based on aspects of trophic ecology, they remain highly clustered around several key trophic strategies.

Although these trends appear inconsistent, they may reflect niche diversification occurring around certain adaptive peaks related to trophic ecology, such as benthic grazer and mid-water carnivore strategies. Rapids within the Xingu River support a high diversity of fishes in the family Loricariidae, many of which are common. While loricariids display considerable variation in trophic traits and isotopic values, their general body form is highly specialized to feed on benthic resources and they tend to occupy lower trophic positions associated with algivorous and detritivorous diets. Although several loricariids (*e.g.*, *Scobinancistrus pariolispos* and *Leporacanthicus heterodon*) possess fewer more robust teeth compared to algivorous species and displayed elevated $\delta^{15}N$ levels associated with partially insectivorous diets (Lujan et al. 2012), they occurred at fewer sites and had little influence on overall patterns. Compared

to species in the remaining eight families analyzed, loricariids have gut lengths, snout lengths, and mouth positions (traits highly correlated with trophic position) that are tightly clustered in a distinct region of functional trait space. This results in a large group of common species with trait values that tend to be widely divergent from trait means, evenly spaced from each other, but clustered together due to shared ancestry and shared reliance on periphyton, detritus, and other benthic resources. Clustering of these traits is also seen in families that tend to occupy higher trophic levels, such as the Cichlidae and Anostomidae, further driving the negative relationship found for SES MNND. Despite the clustering of traits around the benthic grazer and mid-water carnivore strategies, traits more strongly correlated with $\delta^{15}N$ and $\delta^{13}C$ were more evenly spaced, suggesting that mechanisms promoting stabilizing niche differences may have a relatively stronger influence on trophic traits around these adaptive peaks. Consistent with this interpretation, previous studies of assembly patterns in loricariids and cichlids have suggested that these families partition niches along trophic dimensions (Lujan et al. 2012, Montaña et al. 2014); however, the additional tendency towards functional clustering found in the present study highlights how patterns obtained for specific taxonomic groups may differ from assembly patterns found within the larger interacting community.

It is important to emphasize that this analysis provides insights into relative differences in trait dispersion, but not whether overall assembly patterns differ from those expected at random. Physiological and evolutionary tradeoffs may link traits responding to mechanisms promoting functional divergence (*e.g.*, limiting similarity)

with traits responding to even stronger mechanisms promoting functional clustering (*e.*g., environmental filtering, competitive hierarchies), masking the expected patterns of the former. For instance, despite the trend towards more even spacing between trait values with increasing trait correlation with $\delta^{15}N$, most traits have SES values close to zero and are not distinguishable from random patterns. Additional functional tradeoffs exist that are not reflected by variation in trophic ecology (Fig. 5B), and species occurrence may be strongly influenced by mechanisms involving traits associated with other niche dimensions (*e.g.*, habitat use along major environmental gradients), or along multiple dimensions simultaneously (Kraft et al. 2015). Indeed, a recent study by Pool et al. (2016) found that communities with similar functional characteristics often contribute to distinct food web structures. Nevertheless, correlations between functional traits and stable isotope ratios are able to differentiate patterns of trait dispersion after a more general multivariate significance test has been performed, providing further insight into patterns derived from multiple deterministic assembly processes. Additional components of functional variation, such as variation along major environmental gradients (β-niche; Ackerly and Cornwell 2007), could be incorporated through use of the 4^{th} corner problem, RQL analysis, or similar methods designed to correlate traits with environmental characteristics (Dolédec et al. 1996, Dray and Legendre 2008, Brind'Amour et al. 2011). Although data requirements are higher, this approach would be particularly useful for communities thought to partition niches based on habitat use and would complement analyses using stable isotope ratios or alternative measures of ecological performance.

Some have argued that ecological and evolutionary tradeoffs among traits bias analyses based on patterns of individual traits (Verberk et al. 2013). The lack of significant difference between the trophic and habitat-use categories' correlations with isotopic signatures (Fig. 6) emphasizes the importance of identifying trait functions and trait interactions. Although certain Habitat traits, such as caudal peduncle length, anal fin length, and body width, were highly correlated with $\delta^{15}N$, it is unlikely these traits are directly influencing feeding. The long caudal peduncles, fin lengths, and dorso-ventrally compressed bodies of benthivorous loricariids compared to the relatively short caudal peduncles and narrow body widths of many omnivorous/carnivorous species of other families (*e.g.*, *Teleocichla sp.*, *Crenicichla* spp., *Boulengerella cuvieri*) drive this strong correlation. The dorso-ventrally compressed bodies and large fins of benthic fishes, as well as the fusiform shape and slender bodies of mid-water species, are known to influence hydrodynamics in swift water (Lujan and Conway 2015); however, because many of these species also have divergent trophic ecology, these traits were highly correlated with $\delta^{15}N$. Clearly, certain combinations of traits interact to affect species ecological performance, but these trait interactions were reflected in the correlations with isotopic signatures and should not bias results. Understanding of functional roles combined with an objective measure of association between traits and certain niche dimensions should allow for the identification of traits that may be responding disproportionately to processes along those niche dimensions, despite unavoidable tradeoffs and correlations between traits.

This approach provides an effective means to tease apart the influence of multiple assembly mechanisms. Importantly, I would expect no relationship between trait dispersion and trait association with trophic structure within assemblages primarily structured by any single mechanism. For example, no significant relationships were found between SES and trait correlations with $\delta^{15}N$ when analyses were repeated using wet-season data for the same fish assemblages (see *Appendix D*). In many tropical rivers, expansion of aquatic habitat during the wet season leads to lower fish densities and an expected decrease in the strength of species interactions (Winemiller et al. 2014). Previous research on Xingu fishes found that functional diversity of wet-season assemblages was significantly underdispersed compared to null expectations, suggesting that equalizing processes (*e.g.*, environmental filtering) strongly influence these communities along multiple niche axes during the high-water period (see Chapter II).

This analysis revealed that traits strongly associated with trophic structure tend to be more functionally diverse and have more even spacing between values compared to other traits, supporting the idea that certain types of traits respond to assembly mechanisms in predictable ways (Ingram and Shurin 2009, Herben and Goldberg 2014). The large number of studies finding evidence consistent with trophic niche partitioning in fishes suggest that this might be a general trend (Gatz 1981, Ross 1986, Ingram and Shurin 2009, Lujan et al. 2012, Montaña et al. 2014). Additional studies are needed under a variety of hydrologic regimes and river sizes to test the generality of this pattern and how it relates to patterns along other niche dimensions (*e.g.*, habitat use, life history strategies, metabolic strategies). Focusing on individual traits or sets of functionally

interrelated traits may allow for a clearer mechanistic understanding of the assembly process (Spasojevic and Suding 2012, Herben and Goldberg 2014, Trisos et al. 2014, Winemiller et al. 2015); however, the correlated nature of traits and possibility that a single trait may be operating along multiple niche dimensions complicates this approach. The approach presented here offers a promising way to objectively and quantitatively assess trait association with certain niche dimensions, increasing our ability to interpret complex assembly patterns and make hypotheses about general trends in trait-based community assembly.

CHAPTER IV

DIVERSITY AND COMMUNITY COMPOSITION OF RAPIDS-DWELLING FISHES OF THE XINGU RIVER: IMPLICATIONS FOR CONSERVATION

Overview

A recent boom in hydroelectric development in the world's most diverse tropical river basins is currently threatening aquatic biodiversity on an unprecedented scale. Among the most controversial of these projects is the Belo Monte Hydroelectric Complex (BMHC) on the Xingu River, the Amazon's largest clear-water tributary. The design of the BMHC will create three distinctly altered segments: a flooded section upstream of the main dam, a middle section between the dam and the main powerhouse that will be dewatered, and a downstream section subject to flow alteration from powerhouse discharge. This region of the Xingu is notable for an extensive series of rapids known as the Volta Grande that hosts exceptional levels of endemic aquatic biodiversity; yet, little is known about patterns of community composition within this highly threatened habitat. Using fish surveys within rapids in the area impacted by the BMHC prior to hydrologic alteration, I ask whether diversity and community composition differ among the three future impacted zones. I further test whether community composition varies seasonally. While species richness varied only slightly between sections, there were significant differences in community structure between all three sections and between seasons. The dominant compositional pattern observed during all survey periods was the high number of rapids-adapted species found in the

upstream and middle sections. These results further highlight this region of the Xingu as a hotspot of aquatic diversity, and identify the future dewatered section of the Volta Grande as critically important for the conservation of this exceptional fauna. Research is needed to estimate an environmental flow regime to maintain this globally unique habitat and its associated aquatic diversity throughout the lower Volta Grande, and scientists, policymakers, and stakeholders should engage to explore means to implement the prescribed regime.

Introduction

Hydrologic alteration of rivers is widespread, with nearly two-thirds of the world's large rivers impacted by dams (Nilsson et al. 2005). Dams represent one of the greatest threats to aquatic biodiversity worldwide (Vörösmarty et al. 2010); their impacts on flow dynamics and river connectivity cause biotic homogenization, promote invasion of exotic species, favor generalist over specialist species, and increase extinction risk for endemic taxa (Rahel 2000, Johnson et al. 2008, Liermann et al. 2012). Until recently, highly diverse tropical rivers had few large dams (Liermann et al. 2012), but a boom in hydroelectric development in the world's great tropical river basins is now threatening aquatic biodiversity on an unprecedented scale (Zarfl et al. 2015, Winemiller et al. 2016).

The Amazon Basin holds the highest concentration of aquatic biodiversity on the planet, with 2,411 described fish species (roughly 16% of global freshwater fish diversity) and at least 1,089 endemic species (Reis et al. 2016). There are currently 416

dams that are operational or under construction within the basin and an additional 334 have been proposed (Winemiller et al. 2016), which would leave only three free-flowing Amazon tributaries within the next few decades (Fearnside 2006, Castello and Macedo 2016). Existing dams in the Amazon are concentrated in the Tapajós, Tocantins, Xingu, and other tributaries draining ancient granitic shields, which contain more than twice as many endemic species compared to tributaries draining younger Andean regions (Castello and Macedo 2016). In addition to the higher concentration of dams in these tributaries, site selection for development projects generally targets areas with turbulent reaches due to their large hydropower potential. Unfortunately, these same areas often harbor exceptional aquatic diversity.

The Xingu River is the largest clear water-tributary of the Amazon, and contains a unique stretch of river known as the Volta Grande: a 130 km stretch of rapids and anastomosing channels flowing over the crystalline bedrock of the Brazilian Shield (Fig. 7A & B). The river's strong seasonality, steep gradient, and complex geomorphology create substantial habitat heterogeneity that contributes to the maintenance of a globally unique fish fauna (Fig. 7C). Surveys of fish diversity within the basin have identified the Volta Grande as a region of particularly high diversity and endemism (Camargo et al. 2004). Recent surveys in this area have collected over 450 species of fishes in 48 families (Sabaj Pérez 2015), many of which are highly adapted to life within rapids (Zuanon 1999). Of the 63 species known to be endemic to the Xingu Basin (Winemiller et al. 2016), at least 26 are known only from the large rapids complex in the Volta Grande region (Sabaj Peréz et al. unpublished). Although demographic data for many

species are lacking and taxonomic descriptions are ongoing, several species have already been listed as threatened in Brazil (National Red List 2016), including the critically endangered *Hypancistrus zebra* (zebra pleco; Fig. 7C-k), endangered *Hopliancistrus tricornis*, and vulnerable *Ossubtus xinguense* (eagle-beaked pacu; Fig. 7C-c).

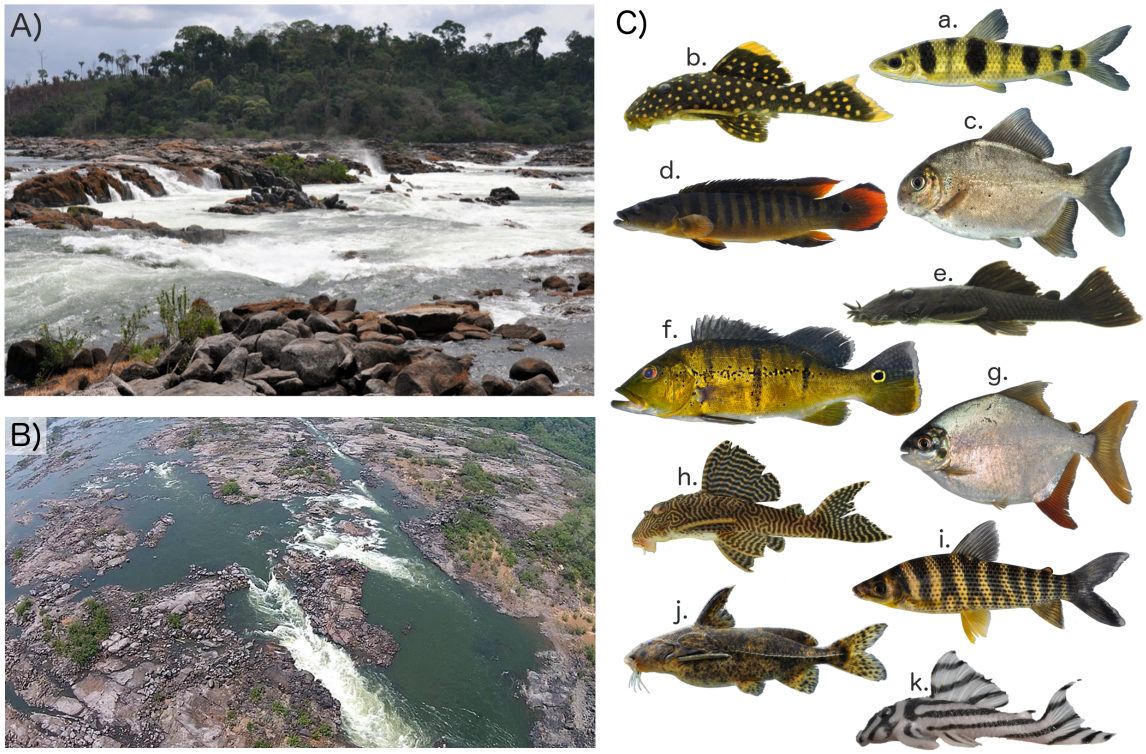

Figure 7. Examples of the habitat (A, B) and fishes (C) characteristic of the Middle Xingu River. Species shown are: a) *Leporinus maculatus* (Anostomidae), b) *Baryancistrus xanthellus* (Loricariidae), c) *Ossubtus xinguense* (Serrasalmidae), d) *Crenicichla sp.* (Cichlidae), e) *Ancistrus ranunculus* (Loricariidae), f) *Cichla melaniae* (Cichlidae), g) *Tometes kranponhah* (Serrasalmidae), h) *Hypancistrus sp.* (Loricariidae), i) *Leporinus tigrinus* (Anostomidae), j) *Rhinodoras sp.* (Doradidae) and k) *Hypancistrus zebra* (Loricariidae). Photos: Mark Sabaj Peréz.

The same factors that promote the tremendous aquatic diversity of the Xingu's Volta Grande also contribute to the hydropower potential of the region, making the middle Xingu the focus of one of the most controversial development projects in the Amazon: the Belo Monte Hydroelectric Complex (BMHC). A massive engineering project, the BMHC is projected to have an installed capacity of 11,233 MW (3rd largest in the world). Initial proposals in 1975 received considerable backlash due to plans for a series of five separate reservoirs within indigenous territories (Fearnside 2006). After intense debate, a redesigned proposal emerged in 2002 focusing on only the dams within the Xingu's Volta Grande region (Fearnside 2006, Sabaj Pérez 2015). Unlike traditional designs that place the powerhouse at the foot of the dam, the new design would take advantage of a large elevation gradient by diverting water through a series of man-made canals to a powerhouse nearly 90 m below. While the new design reduces the size of the reservoirs on nearby indigenous territories, it has the added impacts of dewatering a significant portion of the Volta Grande between the diversion dam and the main powerhouse and flooding hundreds of square-kilometers of forest. Despite continued controversy, accusations of political corruption, and significant cost overruns (Sabaj Pérez 2015, Lees et al. 2016), the Brazilian Environmental Authority authorized the operation of the BMHC on November 24, 2015. The reservoirs are currently filled and two turbines have been generating power commercially since April 20, 2016, with full operation expected by 2019 (Portal Brazil 2016).

Direct impacts of river impoundments are well documented and the BMHC will cause significant and predictable changes to aquatic habitat, resulting in three distinctly

altered stretches. Upstream of the diversion dam, slower water velocities within the impounded reach will result in increased sedimentation (Syvitski et al. 2005), turning the heterogeneous rocky substrate characteristic of this region into a homogenous sandy/muddy bottom. Changes in water depth and water clarity will also alter light penetration, with likely impacts on the availability of benthic resources. Between the diversion dam and the main powerhouse (located 100 km downstream), dewatering of the channel will reduce available aquatic habitat. Flow regulation will reduce seasonal variation (Poff et al. 2007), seasonal access to flooded riparian habitats (Graf 2006), and may alter downstream transport of resources (Syvitski et al. 2005). Downstream of the powerhouse, seasonal variation will also be reduced, with water quality affected by increased erosion from the powerhouse flow and changes in water temperature and dissolved oxygen from reservoir releases.

Limited data on Amazonian aquatic diversity constrains our ability to detect degradation trends and identify conservation priorities (Castello and Macedo 2016). Understanding how fish diversity will respond to expected habitat changes requires data on assemblage composition within the impacted area. Despite the rich aquatic diversity of the Xingu's rapids and the long, controversial history of the BMHC, available data on fish community structure within the region are limited to surveys of slack-water habitats and slower areas adjacent to rapids (Barbosa et al. 2015, Schmid et al. 2016). Because rapids often have distinct fauna that are particularly vulnerable to hydrologic alteration (Lujan and Conway 2015), data on the structure of these fish assemblages throughout the impacted area are urgently needed. To address this, I compared the diversity and

community composition of fishes in rapids of the Middle and Lower Xingu River prior to hydrologic alteration by the BMHC. Specifically, I ask whether fish diversity and local assemblage structure differ between the three future impacted zones (upstream of the diversion dam, middle dewatered section, and downstream of the powerhouse) and how these differences affect conservation and management plans for the river. Because a major impact of river impoundment is reduced seasonal heterogeneity, I further test whether community structure in the main channel differs between high- and low-water periods.

Methods

Data Collection

A 400-km stretch of the Middle and Lower Xingu River surrounding the area to be impacted by the BMHC was surveyed prior to hydrologic alteration (Fig. 8). Three survey periods were selected to represent multiple stages of an annual hydrologic cycle: September 2013 (low water, falling), March 2014 (high water), and November 2014 (low water, rising). Sampling locations were divided into three groups based on anticipated impacts from the BMHC. The 'upstream' section represents the 130-km stretch upstream of the Pimental diversion dam to the confluence of the Xingu and Iriri Rivers that will experience slower flow velocity and lentic conditions within the new impoundment. The 'middle' section represents the 101-km stretch of the Volta Grande between the Pimental Dam and the Belo Monte powerhouse that will experience greatly reduced flows. The 'downstream' section represents the 171-km stretch downstream of

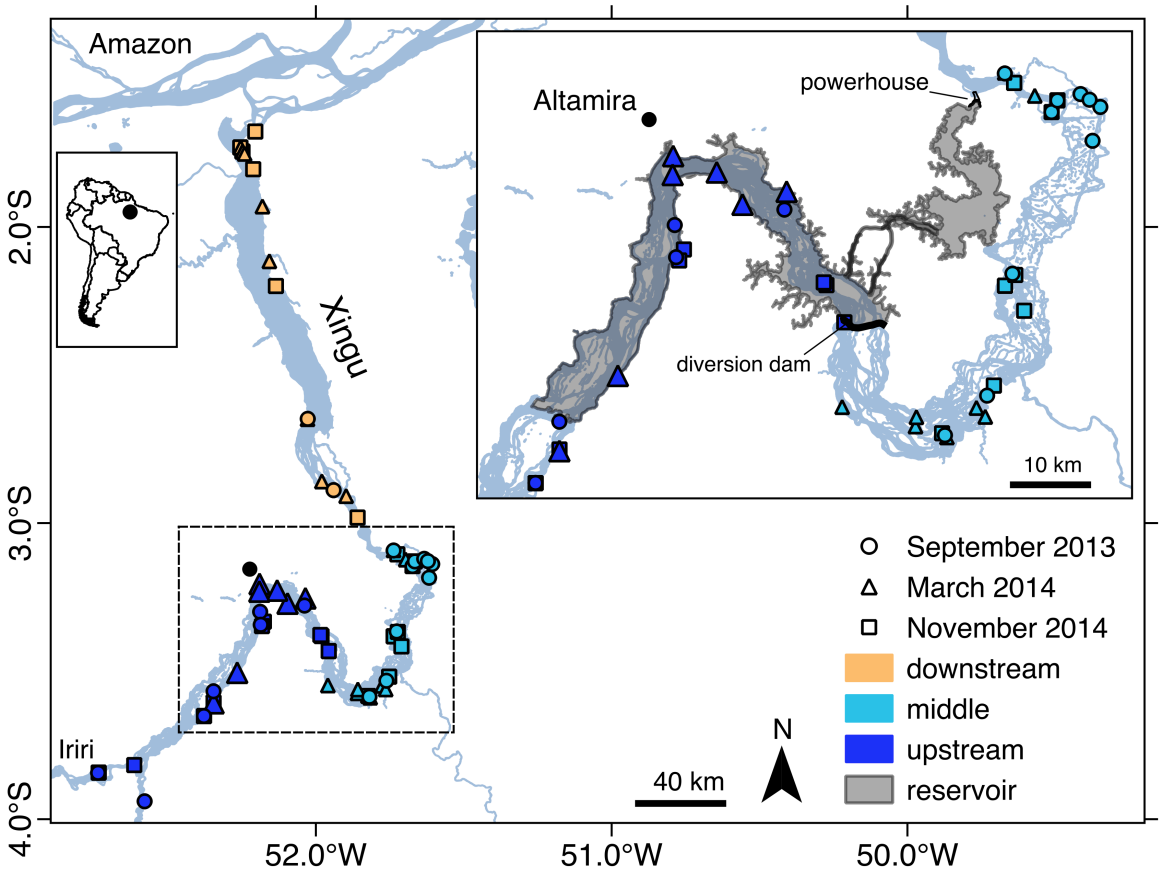

Figure 8. Map of study region showing sampling locations for three survey periods and three river sections. Area altered by the Belo Monte Hydroelectric Complex shown in inset. Water flow is generally northern.

the Belo Monte powerhouse to the confluence of the Xingu and Amazon Rivers that will receive outflow from the BMHC. The number of sites surveyed within each section during each sampling period is provided in Table 3.

Surveys targeted shallow rapids and deep, swift water over rocky substrates within channels of the principal river course. Water velocity ranged from 0–4.4 m/s. Each sampling location received 60–80 minutes of fishing effort over an area of approximately 100 m^2. Fishes were collected by hand by experienced divers who work

Table 3. Number of sites surveyed.

	River Section			
Survey	Upstream	Middle	Downstream	Total
SEP 2013	8	10	8	26
MAR 2014	11	9	11	31
NOV 2014	15	13	10	38

in the ornamental fish trade. This technique primarily targets benthic species, though some highly mobile species were also collected. The same two divers sampled all sites, with the exception of sites upstream of Altamira in March 2014, when an alternative diver replaced one of them.

Data Analysis

Sample-size based rarefaction/extrapolation curves were used to compare species richness between the three sections. Because taxonomic work in the basin is ongoing (at least 23 new fish species described since 2008), easily distinguished morphological variants of some described species (*e.g.*, *Spectracanthicus punctatissimus*, Loricariidae) were treated as distinct species for this analysis (see *Appendix E*). Rarefaction was conducted separately for each survey period following methods developed by Colwell et al. (2012) implemented within the package iNEXT (Chao et al. 2014) using R version 3.2.2 for OS X (R Core Team 2015).

To compare dominant trends in community structure between sections, I first removed rare species and any species collected at a single site. For the 2013 low-water period, rare species were defined as those with less than 4 individuals, leaving 82 species accounting for 89.9% of fish abundance in samples. Due to lower number of species

collected in the remaining two survey periods, rare species were defined as singletons, leaving 54 species accounting for 80.4% of abundance during the 2014 high-water period and 34 species accounting for 88.7% of abundance during the 2014 low-water period.

Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations was used to test for differences in community composition between sections and Non-metric Multidimensional Scaling (NMDS) was used to visualize differences in sites between sections. NMDS was based on standardized relative abundances fitted to 6 axes; a scree plot was used to select the lowest number of axes without substantial increase in stress, though choice of fewer dimensions produced similar results. Principal Components Analysis was then used to display the two dominant NMDS axes. Euclidean distance between geographic coordinates of sites was used as a starting configuration for the iterative procedure. Finally, a two-way cluster analysis following Ward's D method for hierarchical clustering was used to explore patterns of species composition across sites within each survey period. All community analyses were based on relative abundance data and Bray-Curtis distances, and were performed using the package vegan in R (Oksanen et al. 2015).

To test for differences in species composition during low- and high-water periods, the 2013 and 2014 low-water surveys were combined and compared with the 2014 high-water period. Rare species were defined as those with less than 4 individuals in the combined datasets and PERMANOVA and NMDS were performed as described above.

Results

A total of 8,059 individuals representing 248 species and 23 families was sampled during the three survey periods (*Appendix E*), with samples dominated by species of the families Loricariidae (68 spp.), Characidae (43 spp.), Cichlidae (30 spp.), Anostomidae (18 spp.), and Doradidae (14 spp.). The upstream and middle sections each contained 141 species, whereas 102 species were sampled in the downstream section. Rarefaction analysis showed that species richness was highest in the upstream section during the two low-water survey periods (Fig. 9A & C), although 95% confidence intervals of rarefied curves for upstream and downstream sections overlapped during the 2014 low-water period. During the 2014 high-water survey, the middle section had higher species richness than the upstream section, but confidence intervals for the downstream section overlapped with both (Fig 9B).

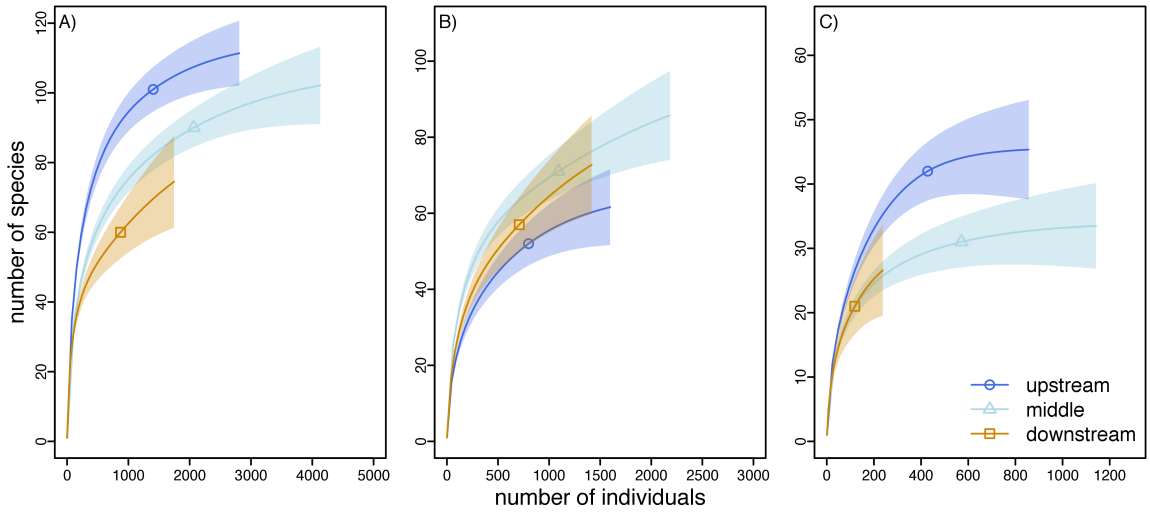

Figure 9. Rarefaction/extrapolation curves for A) low water September 2013, B) high water March 2014, and C) low water November 2014. Symbols represent actual number of sampled individuals and species for each section. Shaded regions represent 95% confidence intervals for interpolated (left of symbol) and extrapolated (right of symbol) curves.

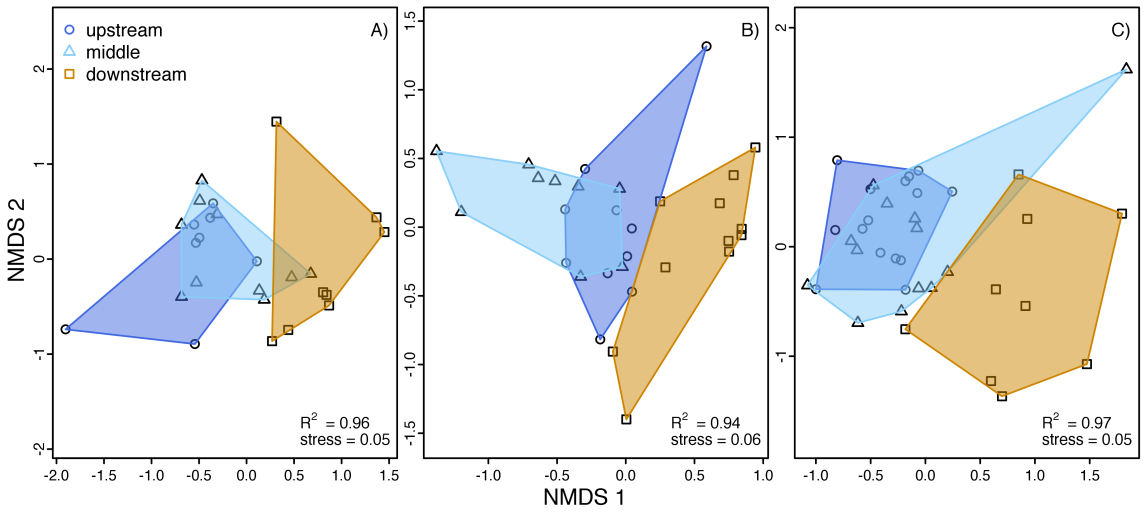

Figure 10. Non-metric multidimensional scaling results for A) low water September 2013, B) high water March 2014, and C) low water November 2014 based on species relative abundance at sampling sites. Symbols represent sites and shaded polygons are convex hulls for the three river sections.

Community composition differed significantly between river sections during all survey periods (PERMANOVA; low water 2013: $F_{(2,23)} = 2.07$, $P = 0.001$; high water 2014: $F_{(2,27)} = 1.89$, $P = 0.001$; low water 2014: $F_{(2,34)} = 2.33$, $P = 0.001$). NMDS revealed partial overlap of the upstream and middle sections and clear separation of the downstream section (Fig. 10). Similarity of the upstream and middle sections was influenced by a core group of species with high relative abundances in both sections, and that were either absent or present at low relative abundances in the downstream section (Fig. 11; *Appendix F*). This group included *Baryancistrus xanthellus*, *Hypancistrus zebra*, *Scobinancistrus aureatus* (Loricariidae), *Hypomasticus julii*, *Leporinus maculatus*, *Leporellus vitatus* (Anostomidae), *Cichla melaniae* (Cichlidae), and *Corydoras xinguensis* (Callichthyidae). The distinctness of the upstream section was

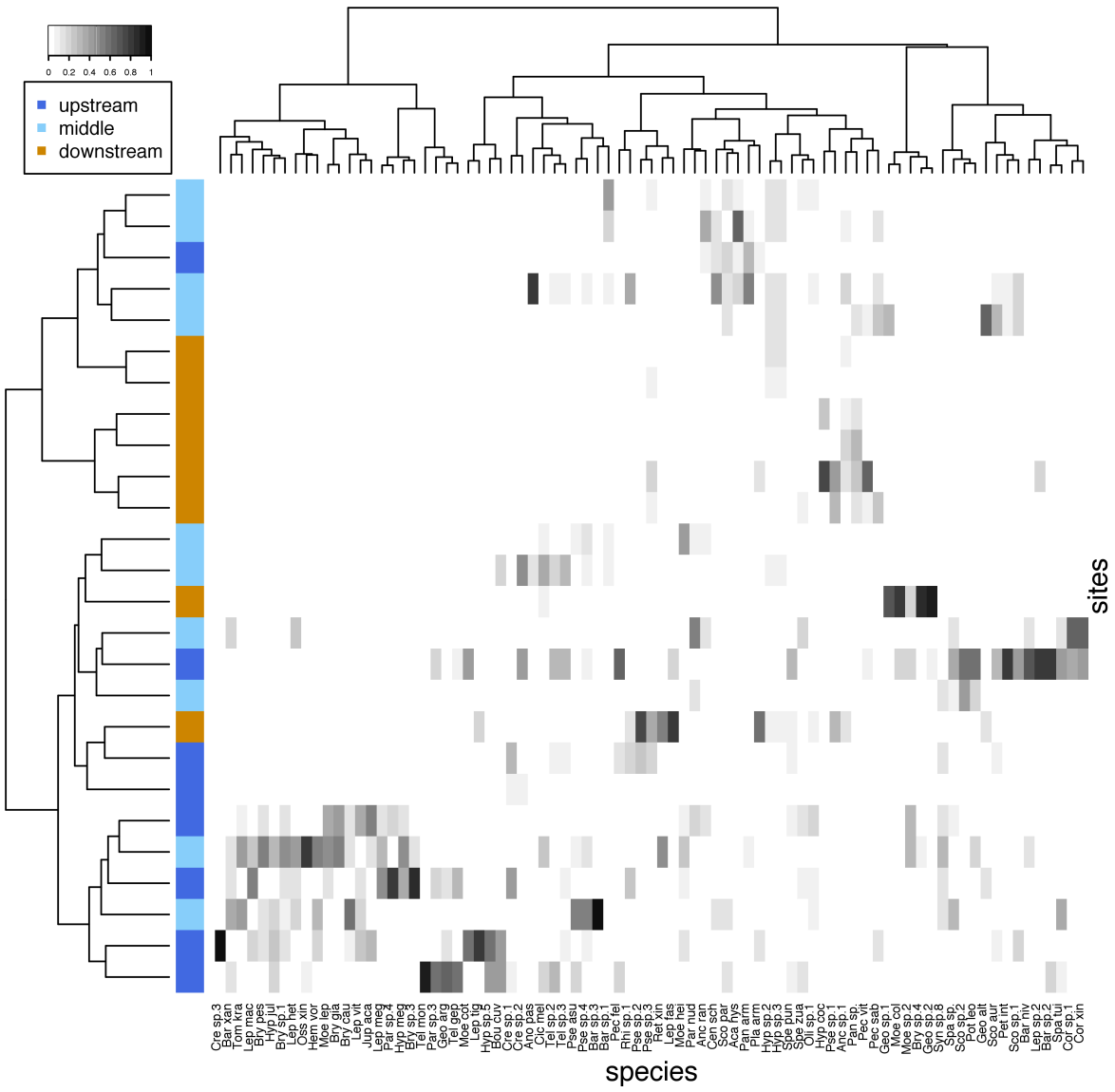

Figure 11. Two-way cluster analysis of low-water (September 2013) assemblages. Clustering follows Ward's D, using Bray-Curtis dissimilarity matrix based on species relative abundances. Colors along edge represent river sections and grey-scale shading within represents species relative abundance at a given site. Species abbreviations and two-way cluster analyses for remaining sampling periods are provided in *Appendices E* and *F*, respectively.

driven by species such as *Crenicichla percna* (Cichlidae) and *Parancistrus sp*.

(Loricariidae), while species such as *Baryancistrus sp*., *Hopliancistrus tricornis*

(Loricariidae), *Anostomoides passionis*, and *Pseudanos trimaculatus* (Anostomidae) were only sampled in the middle section. The middle section was further distinguished from the upstream section by species found at higher relative abundances, such as *Ossubtus xinguense* (Serrasalmidae) and *Ancistrus ranunculus* (Lorcariidae).

The clear separation of the downstream section was due to a large group of species only sampled in this section, such as *Crenicichla reticulata*, *Cichla pinima* (Cichlidae), *Hypostomus plecostomus*, *H. cochliodon* (Loricariidae), *Centrodoras sp*., and *Megalodoras uranoscopis* (Doradidae). Several species were found at sites throughout the study region, such as *Spectracanthicus punctatissimus*, *S. zuanoni*, *Peckoltia vittata*, *P. sabaji*, *Hypancistrus sp.* (Loricariidae), *Geophagus agyrostictus*, *Retroculus xinguense* (Cichlidae), and *Leporinus fasciatus* (Anostomidae), though relative abundances varied between sections.

Species composition differed significantly between low- and high-water periods (PERMANOVA: $F_{(2,92)} = 1.89$, $P = 0.001$), with 114 species sampled only during low-water surveys and 56 species sampled only during the 2014 high-water survey. In general, species sampled in the main channel under high water conditions were a subset of those found during low-water periods (*Appendix F*). The common loricariids were sampled during both seasons, but several less common species were collected only during low-water periods (*e.g*., *Baryancistrus sp.*, *Acanthicus sp*.) or high water (*e.g*., *Ancistrus sp*., *Spectracanthicus sp.*, *Limatulichthys punctatus*). Numerous species of characids, cichlids, and anostomids were sampled only during low-water periods. Most

species sampled only at high water were relatively rare, including several species of *Centromochlus* (Auchinipteridae) and *Sternarchorhyncus* (Apteronotidae).

Discussion

Species richness was similar between the three sections when all survey periods were combined; however, it is important to note that the middle section had similar diversity within a shorter stretch of river. The higher richness observed during low-water periods in the upstream section compared to the middle section is likely due to its longer length, which includes the upper half of the highly diverse Volta Grande. The downstream section contained similar species richness as the dewatered section during all survey periods, despite being roughly 70 km longer. These results further highlight the Volta Grande as a hotspot for fish diversity within the Xingu Basin. The lower species richness found in the upstream section during the high-water period may be an artifact due to dangerous conditions in many of the rapids within this area, as well as a change in one of the divers sampling these locations.

A dominant pattern observed throughout all survey periods is the high number of rapids-adapted species found in the upstream and middle sections. Faunal similarity of these sections was influenced by many shared rheophilic species (Zuanon 1999), such as *Parancistrus nudiventris* (Rapp Py-Daniel and Zuanon 2005), *Tometes kranponhah* (Andrade et al. 2016), and *Ossubtus xinguense* (Jegu and Zuanon 2005). Downstream, many rheophilic species are replaced by species that are more habitat generalists and species common throughout the Lower Amazon River. Species turnover along fluvial

gradients generally corresponds to discontinuities in stream geomorphology and/or abiotic conditions (Jackson et al. 2001). The geomorphology of the upstream and middle sections consists of numerous braided channels and extensive shallow rapids flowing over crystalline bedrock of the Brazilian Shield. Downstream, the Xingu leaves the shield and forms a singular channel flowing through the alluvial reach of the Lower Amazon River (Sabaj Pérez 2015). Water velocities in the downstream section remain high, but rocky substrates occur in patches and are deeply submerged. This transition in river geomorphology likely accounts for the distinct community compositions above and below Belo Monte and may partly explain the high endemism found within the Volta Grande. The same pattern of distinct community structures between the middle and lower Xingu River was found in gill net surveys of slack-water habitats (Barbosa et al. 2015), suggesting that this may be a general pattern for fish diversity in the Xingu.

Obligate rheophilic species that inhabit shallow rapids in the upstream and middle sections are most susceptible to impacts from hydrologic alteration (Lujan and Conway 2015). Within the upstream section, the reservoir will eliminate huge areas of rapids habitat. Reduced species richness has been documented following construction of reservoirs in other regions of the Amazon (Sá-Oliveira et al. 2015), and reservoirs in both Neotropical and temperate regions are often dominated by a few generalist species (Rahel 2000, Agostinho et al. 2008). Many rheophilic fishes will likely be extirpated from the upstream section. Regional persistence will depend on both availability of suitable habitat and dispersal ability, which varies widely across taxa. For example, some loricariids (the most diverse and abundant family within the rapids) display

ontogenetic movements, but are generally highly sedentary compared to most other fishes, such as anostomids and serrasalmids (Lucas and Baras 2001).

Species unable to disperse will face numerous challenges within the newly impounded upstream section. Habitat complexity has been shown to positively influence freshwater fish diversity by providing enhanced foraging opportunities and lower predation risk (Jackson et al. 2001, Arrington et al. 2005, Willis et al. 2005, Schneider and Winemiller 2008). Increased sedimentation due to slower water velocities will fill interstitial spaces within structurally complex rocky substrates, reducing opportunities for niche partitioning, refuges from predators, and availability of suitable breeding sites, with likely decreases in local diversity. Several common species inhabiting rapids of the Xingu River are mainly supported by benthic algae (Zuluaga Gómez et al. 2016). Changes in water depth, clarity, and temperature may alter the availability of this resource for algivorous fishes. Indeed, studies of Amazonian reservoirs have found dominance of omnivorous and carnivorous species (Sá-Oliveira et al. 2015), making the future of specialist primary consumers in the upstream section uncertain. Reduced concentrations of dissolved oxygen at the bottom of the reservoir may place additional metabolic stress on the numerous benthic fishes adapted to the highly oxygenated rapids characteristic of the Xingu.

Species present in the middle section will face a very different set of challenges. Maintenance of aquatic biodiversity requires both base flow to provide sufficient habitat and periodic flow pulses that influence geomorphological dynamics and a host of critical ecological processes. The annual flood pulse is the primary environmental driver of

tropical rivers, influencing biotic interactions, access to productive floodplain habitats, and timing of reproductive and migratory patterns (Junk et al. 1989, Lucas and Baras 2001, Winemiller et al. 2014). Current estimates of the flow that will remain throughout the dewatered section range between 17–25% of mean total annual discharge, significantly reducing the wetted area of the channel (see supporting information in Stickler et al. 2013). The Pimental diversion dam will greatly reduce seasonal and inter-annual variation, removing a key component of the system's heterogeneity. Community assembly dynamics in the Xingu have been shown to vary seasonally, with decreased influence of biotic interactions during the high-water period likely playing a role in maintaining diversity (Chapter II). Reduced seasonal dynamics in the dewatered portion and greater competition for remaining aquatic space year-round may lead to both reduction of diversity due to competitive displacement and significant changes in community structure. Species that rely on flooded riparian forests will lack access to vital resources, such as terrestrial food subsidies and seasonal breeding sites. The seasonal differences in community structure observed in this study may be partly explained by differences in sampling efficiency, but the absence of many anostomids, characids, and serrasalmids from main channel habitats during the wet season could have been due to their lateral migrations into flooded habitats (Lucas and Baras 2001). In addition, the combination of reduced flow and the Pimental impoundment will greatly reduce the ability of longitudinal migrants to navigate the channel. Fish ladders have been installed at Pimental, but these have proven ineffective as a mitigation strategy for

other Neotropical impoundments (Pompeu et al. 2012) and will not aid species trying to navigate the dewatered rapids and waterfalls of the lower Volta Grande.

Fishes inhabiting deep rocky areas of the downstream section tended to be wide-ranging and environmentally tolerant; however, several rapids-associated species are still present in this section. The outflow from the main powerhouse will maintain sufficient discharge, though the attenuated seasonal variability will create similar impacts to those discussed above. In addition, changes in thermal profile, oxygen content, and nutrient levels due to reservoir releases may disproportionately affect clear-water species with narrow environmental tolerances, shifting community structure towards a even greater influence of lowland Amazonian species.

The presence of such a unique assemblage of rapids-adapted species in the upstream and middle sections clearly highlights these stretches as conservation priorities. Because the in-stream reservoir is necessary for the hydropower potential of the BMHC, there is little that can be done for the conservation of rapids habitats in the upstream section. In fact, the two reservoirs currently built are projected to generate only a fraction of the full BMHC capacity, leaving many to speculate that developers will leverage this to build additional impoundments further upstream as originally proposed (Fearnside 2006, Stickler et al. 2013). This pressure will only increase given the projected decline in discharge for the Xingu due to continued deforestation in the region (Stickler et al. 2013). While conservation efforts should continue to resist development of additional dams upstream, it is clear that conserving the fish diversity and endemism

currently found throughout the study reach will depend critically on how the dewatered portion of the Volta Grande is managed.

Allowing for a dynamic flow regime will be critical to maintaining diversity within the dewatered section. Average monthly discharge in the Xingu River near Altamira ranged from 1,110–20,617 m^3/s during the period 1971–2015, with peak high-water discharges ranging from 9,861–30,112 m^3/s (HidroWeb 2015). Ideally, releases from the Pimental impoundment would mimic not only the seasonal dynamic, but incorporate the over 20,000 m^3/s of inter-annual variability observed in peak high-water discharge. The sustainability boundaries approach to determining environmental flows (Richter 2009), in which requirements are expressed as allowable percentages of deviation rather than particular volumes at given times of year, would aid in maintaining flow dynamics throughout the lower Volta Grande and lower Xingu. Determining appropriate boundaries is a difficult process that is beyond the scope of this chapter, but the roughly 80% reduction currently expected will likely leave insufficient flows for the maintenance of aquatic diversity.

Protection from further disruption in the dewatered area will be essential. The Canadian mining company Belo Sun has been granted a 1,305 km^2 concession to build Brazil's largest gold mine in the dewatered channel, immediately downstream of the Pimental diversion dam (Lees et al. 2016). Draft legislation allowing mining operations in protected areas and indigenous lands in Brazil (Mining Code Bills 37/2011, 3682/2012, and 1610/96) will open the doors to further expansion within the adjacent Paquiçamba and Arara Indigenous territories. Gold mining has had significant effects on

water quality, biodiversity, and environmental/human health along other Amazonian rivers (Swenson et al. 2011), and significant efforts must be made to block such developments from the dewatered stretch of the Volta Grande.

Continued environmental monitoring will be needed to manage aquatic biodiversity post hydrologic-alteration. Monitoring efforts for fishes are in place (Barbosa et al. 2015), but should be expanded to include additional components of aquatic biodiversity, riparian forest cover, and impacts on local livelihoods. In addition, non-invasive monitoring approaches should be explored and implemented where possible (Schmid et al. 2016). Captive breeding programs have been initiated for several species of conservation concern, including the critically endangered *Hypancistrus zebra* (zebra pleco); however, these strategies do little to promote conservation of critical habitat for remaining species. While hydrological methods for determining flow downstream of the diversion dam can be used initially, studies on habitat requirements of target species or assemblages will be necessary for more sophisticated habitat simulation or holistic approaches for generating optimum flow recommendations in the future (Tharme 2003).

The Middle Xingu has been described as a "river of rivers" (Sabaj Pérez 2015), where channels approximating the geomorphology of small streams are interwoven with those of more typical higher-order channels. Undoubtedly, this complexity is partly responsible for the aquatic diversity currently found there, making it imperative to maintain the variety and amount of flow necessary to sustain this globally unique habitat throughout the remainder of the Volta Grande.

CHAPTER V

CONCLUSION

The ultimate goal of community ecology, and particularly of functional trait-based approaches like those presented in Chapters II and III, is to identify general rules that offer predictive capabilities (McGill et al. 2006). The predictive power of the trait-based approach will depend on the degree of consistency in trait response to a given mechanism. The studies presented in the preceding chapters clearly highlight the dynamic nature of the assembly process, suggesting that patterns of functional diversity depend on both the environmental conditions present and the specific traits analyzed. Continued progress towards a predictive theory of community assembly must therefore incorporate temporal variation as well as consider potential differences across major niche axes.

The relative influence of assembly mechanisms may vary temporally, such that patterns of species co-occurrence depend on the period of sampling. Comparison of observed functional diversity revealed that wet-season assemblages are more functionally similar than dry-season assemblages. Further, wet-season assemblages were more functionally similar than random expectations based on comparison with null model predictions. Higher functional richness in dry-season communities is consistent with increased niche complementarity during a time when biotic interactions are stronger; however, null model results suggest that stochastic factors or a combination of assembly mechanisms operate during the dry season. These results demonstrate that the

relative influence of community assembly mechanisms vary seasonally in response to changing abiotic conditions. Expanded habitat and decreased density of aquatic organisms during the wet season may limit the influence of biotic assembly mechanisms, including competitive exclusion, which might partially explain the extraordinary fish diversity present in the Xingu River.

The relative influence of different assembly mechanisms may also vary depending on the particular traits analyzed. A significant relationship was found between a trait's deviation from null expectations and its correlation with isotopic patterns, with traits strongly associated with trophic ecology displaying greater dispersion from the mean and more even spacing of trait values. Greater packing of traits associated with trophic ecology indicated that stabilizing niche differences occur around adaptive peaks. These results suggest that traits associated with trophic ecology are more influential in niche differentiation affecting species coexistence, and demonstrate that certain traits may respond to assembly mechanisms in predictable ways despite the complex, multidimensional nature of the assembly process (Ingram and Shurin 2009, Herben and Goldberg 2014). Furthermore, the large number of studies finding evidence consistent with trophic niche partitioning in fishes suggest that this might be a general trend (Gatz 1981, Ross 1986, Ingram and Shurin 2009, Lujan et al. 2012, Montaña et al. 2014).

Empirical tests of trait distributions, such as those presented in Chapters II and III, offer a path towards developing robust hypotheses of the factors driving ecological community assembly. Expanding these tests across a variety of habitats and environmental conditions will be a critical step in exploring the generality of specific

patterns; however, additional experiments and comparative studies will be needed to explicitly test potential underlying mechanisms and elucidate trait functions. Yet, even in the absence of explicit tests of underlying mechanisms, discovery of general patterns may aid efforts to conserve biodiversity and manage fisheries resources. Combined with the spatial analysis conducted in Chapter IV, the results of this dissertation will help establish priorities for conservation efforts within the Xingu.

While species richness varied only slightly between river sections, there were significant differences in community structure. The dominant compositional pattern observed was the high number of rapids-adapted species found in both the section that will be impounded and the section that will be dewatered. These results further highlight the Xingu's Volta Grande as a hotspot of aquatic diversity, and suggest the future dewatered section of the Volta Grande will be critically important for the conservation of this unique fauna. Maintaining a dynamic flow regime that includes key components of the historic hydrograph, as well as concerted efforts to limit further disruption in the dewatered channel or adjacent riparian areas, will be essential to maintaining this globally unique habitat and its associated diversity. Ideally, releases from the Pimental impoundment and Belo Monte powerhouse would mimic not only the seasonal dynamic, but also incorporate inter-annual variability. The sustainability boundaries approach (Richter 2009) could be useful for estimating environmental flow needs for the lower Volta Grande and lower Xingu. Determining appropriate boundaries is a difficult process that is beyond the scope of this dissertation, but the roughly 80% reduction

currently expected will undoubtedly result in insufficient flows for the maintenance of aquatic diversity and livelihoods of local riparian communities.

Environmental monitoring will be critical for detecting degradation trends and identifying conservation priorities (Barbosa et al. 2015, Castello and Macedo 2016), but additional studies will be required to fill key gaps in our knowledge of Xingu fish ecology. For example, studies of specific habitat requirements of target species or assemblages will be necessary for use of habitat simulation or holistic approaches for generating optimum flow recommendations (Tharme 2003). This dissertation adopted assembly theory as a basis to explore fish community ecology, but additional perspectives such as food web theory would provide complimentary information for managers. A large database of stable isotope ratios has been assembled in conjunction with the data presented in Chapter III, which will be used in future studies exploring food web structure and dynamics within the Middle and Lower Xingu (*e.g.*, see Zuluaga Gómez et al. 2016). In addition, genetics studies would facilitate both taxonomic research in the basin and help identify important pathways of gene flow in the region.

The task of conserving/managing nearly 500 species of fish is daunting. While a community ecology perspective can aid this process, there is still much to learn about the ecology of the Xingu. A precautionary approach focused on maintaining sufficient habitat and major sources of environmental heterogeneity will go a long way towards protecting biodiversity in the region while critical baseline data are analyzed and new data are collected. The Xingu's Volta Grande region has been described as a "river of rivers" (Sabaj Pérez 2015), where channels approximating the geomorphology of small

streams are interwoven with those of more typical higher-order channels. Undoubtedly, this spatial complexity and temporal variation in flow are essential for maintaining the globally unique aquatic diversity of the Xingu's Volta Grande.

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APPENDIX A

SPECIMEN LIST – CHAPTER II

Table A 1. List of specimens used in Chapter II analyses. All specimens are stored in the ichthyology collection of the Academy of Natural Sciences of Philadelphia (ANSP). Catalog numbers refer to lots of one or more individuals from the same sampling event; tissue numbers represent unique identification numbers for individual specimens within lots.

Family	Species	Catalog No.	Tissue No.
Anostomidae	*Hypomasticus julii*	ANSP 194748	t0435
			t0436
			t0437
	Hypomasticus megalepis	ANSP 194751	t0443
			t0447
			t0518
	Leporinus maculatus	ANSP 194750	t0517
		ANSP 194774	t0547
		ANSP 194810	t0207
	Leporinus aff. *fasciatus*	ANSP 194817	NA
	(Tapa-Xingu)	ANSP 194900	t1160
			t1162
	Pseudanos trimaculatus	ANSP 194641	NA
			NA
			t1050
Apteronotidae	*Sternarchorhynchus* sp.	ANSP 194950	t1010
		ANSP 196430	t2254
		ANSP 196466	NA
Characidae	*Brycon* aff. *pesu*	ANSP 194652	NA
		ANSP 194766	t0549
			t0550
	Moenkhausia heikoi	ANSP 194970	NA
			t1515
			t1516
	Moenkhausia lata/*xinguensis*	ANSP 194549	t1323
		ANSP 195041	t1584
			t1585
Cichlidae	*Cichla pinima*	ANSP 194089	t1095
		ANSP 194454	t1194
		ANSP 194524	t1280
	Crenicichla sp. (xingu 1)	ANSP 194647	t0124

Table A 1. Continued.

Family	Species	Catalog No.	Tissue No.
Cichlidae	*Crenicichla* sp. (xingu 1)	ANSP 194803	t0242
		ANSP 194995	NA
	Crenicichla sp. (xingu 2)	ANSP 194912	t0967
			t0968
		ANSP 196400	t2083
	Geophagus sp. (common high back)	ANSP 197513	t2329
			t2343
			t2349
	Teleocichla centrarchus	ANSP 194697	t1543
		ANSP 196390	t2713
		ANSP 196409	t2075
	Teleocichla sp. (black)	ANSP 194828	t0266
		ANSP 194895	t1557
		ANSP 194913	t0980
Ctenoluciidae	*Boulengerella cuvieri*	ANSP 195266	t2420
			t2421
			t2424
Doradidae	*Platydoras* cf. *armatulus*	ANSP 194904	t1071
			t1073
			t1074
	Rhinodoras sp.	ANSP 194808	t0248
		ANSP 194893	t1570
		ANSP 194907	t1076
Hemiodontidae	*Hemiodus vorderwinkleri*	ANSP 194700	t1494
			t1495
		ANSP 194771	t0553
Loricariidae	*Acanthicus histrix*	ANSP 194882	t1545
			t1547
		ANSP 194953	NA
	Ancistrus ranunculus	ANSP 194841	t0325
		ANSP 194955	t0907
		ANSP 194969	t1520
	Baryancistrus xanthellus	ANSP 194814	t0212
		ANSP 194851	t0314
			t0334
	Hopliancistrus tricornis	ANSP 194663	t0137
			t0138
			t0139

Table A 1. Continued.

Family	Species	Catalog No.	Tissue No.
Loricariidae	*Hypancistrus* sp. (L333)	ANSP 194643	t1041
			t1042
			t1046
	Hypostomus sp.	ANSP 194539	t1311
		ANSP 194649	t0161
		ANSP 194838	t0323
	Leporacanthicus heterodon	ANSP 194749	t0458
		ANSP 194870	t0938
		ANSP 194940	t0756
	Panaqolus sp.	ANSP 194631	t1255
			t1260
		ANSP 194790	NA
	Panaque armbrusteri	ANSP 194864	t0381
		ANSP 194890	t1567
			t1568
	Parancistrus aff. aurantiacus	ANSP 194495	t1524
		ANSP 194824	t0293
			t0294
	Peckoltia feldbergae	ANSP 194656	t0143
			t0144
		ANSP 194833	t0288
	Peckoltia sabaji	ANSP 194637	t1019
		ANSP 194846	t0330
		ANSP 194891	t1550
	Peckoltia vittata	ANSP 194632	t1256
		ANSP 194638	t1026
			t1027
	Pseudacanthicus sp. (L25)	ANSP 194906	t1079
			t1081
			t1083
	Pseudancistrus asurini	ANSP 194658	t0148
		ANSP 194760	t0470
		ANSP 194892	t1463
	Scobinancistrus pariolispos	ANSP 194654	t0131
		ANSP 194894	t1551
		ANSP 194962	t1638
	Spatuloricaria tuira	ANSP 194651	t0183
		ANSP 194873	t0910
		ANSP 194939	t0754
	Spectracanthicus punctatissimus	ANSP 194552	t1314

Table A 1. Continued.

Family	Species	Catalog No.	Tissue No.
Loricariidae	*Spectracanthicus punctatissimus*	ANSP 194552	t1315
		ANSP 194834	t0297
		ANSP 194813	t0225
			t0226
		ANSP 194877	t0946
	Spectracanthicus zuanoni	ANSP 194812	t0215
			t0220
		ANSP 194944	t0741
	Squaliforma sp. (Xingu)	ANSP 194784	t0573
			t0582
		ANSP 194957	t1142
Serrasalmidae	*Ossubtus xinguense*	ANSP 193060	NA
		ANSP 194758	t0502
			t0505
	Tometes kranponhah	ANSP 194419	t0805
		ANSP 194763	t0514
			t0515

APPENDIX B

FUNCTIONAL TRAIT DEFINITIONS

Table B 1. Functional traits measured. All linear distances measured to the nearest 0.01 mm using digital calipers and angular distances measured to the nearest degree using a protractor. Trait definitions and categories follow Gatz (1979), Winemiller (1991), Delariva and Agostinho (2001), Pease et al. (2012), and Lujan and Armbruster (2012).

Category	Trait	Code	Definition	Transformation[¥]
Habitat	Maximum standard length	max.sl	Maximum standard length from the populations in this study	Log
	Body depth	bod.d	Maximum vertical distance from dorsum to ventrum	Log
	Body width	bod.w	Maximum horizontal distance from side to side	Log
	Mouth position	mou.p	The angle between an imaginary line connecting the tips of the open jaws and an imaginary line running between the center of the pupil and posterior-most vertebra (*e.g.*, 90˚ representing a terminal mouth)	Log
	Eye position	eye.p	Vertical distance from the center of the pupil to the ventrum	Log
	Eye diameter	eye.d	Horizontal distance from eye margin to eye margin	Square root
	Caudal peduncle length	ped.l	Distance from the posterior proximal margin of the anal fin to the caudal margin of the ultimate vertebra	Cube root
	Caudal peduncle depth	ped.d	Minimum vertical distance from dorsum to ventrum of caudal peduncle	
	Caudal peduncle width	ped.w	Horizontal width of caudal peduncle at mid-length	Square root
	Body depth below midline	bdbm	Vertical distance from midline to ventrum, midline defined as the imaginary line passing through the pupil and the center of the ultimate vertebra	
	Dorsal fin length	dors.l	Distance from the anterior proximal margin to the posterior proximal margin of the dorsal fin	Square root
	Dorsal fin height	dors.h	Maximum distance from the proximal to distal margin of the dorsal fin, excluding filaments	

Table B 1. Continued.

Category	Trait	Code	Definition	Transformation[¥]
Habitat	Anal fin length	anal.l	Distance from the anterior proximal margin to the posterior proximal margin of the anal fin	Inverse
	Anal fin height	anal.h	Maximum distance from the proximal to distal margin of the anal fin, excluding filaments	Log
	Caudal fin depth	caud.d	Maximum vertical distance across the fully spread caudal fin	
	Caudal fin length	caud.l	Maximum distance from the proximal to distal margin of the caudal fin, excluding filaments	
	Pectoral fin length	pect.l	Maximum distance from the proximal to distal margin of the pectoral fin, excluding filaments	Log
	Pectoral fin height	pect.h	Maximum vertical distance across the fully spread pectoral fin	
	Pelvic fin length	pelv.l	Maximum distance from the proximal to distal margin of the pelvic fin, excluding filaments	
Trophic	Head length	head.l	Distance from the tip of the lower jaw to the posterior edge of the operculum	
	Head depth	head.d	Vertical distance from dorsum to ventrum passing through the pupil	Log
	Mouth height	mou.h	Vertical distance measured inside of fully open mouth at tallest point	
	Mouth width[*]	mou.w	Horizontal distance measures inside of fully open mouth and widest point	
	Snout length closed[*]	snl.c	Distance from the pupil to the tip of the upper jaw with mouth shut	
	Snout length open[*]	snl.o	Distance from the pupil to the tip of the upper jaw with mouth open and fully extended	
	Mouth protrusion	mou.pro	Distance from the pupil to the tip of the upper jaw with mouth shut, divided by Distance from the pupil to the tip of the upper jaw with mouth open and fully extended	Inverse
	Gut length	gut.l	Length of gut from the beginning of the esophagus to the anus, extended without stretching	Log
	Gill raker length	rakr.l	Length of the longest gill raker	Cube root

Table B 1. Continued.

Category	Trait	Code	Definition	Transformation[¥]
Trophic	Tooth shape	tooth.s	Horizontal distance between tooth edges measured at tip of crown of longest tooth (taken as zero for pointed, triangular shaped teeth) divided by horizontal distance measured at base.	Square root
	Number of upper teeth	teeth.u	Number of teeth located on the maxilla	Square root
	Number of lower teeth	teeth.l	Number of teeth located on the mandible	Cube root
	Tooth length upper	tooth.l.u	Vertical distance from base of crown to tip of tooth measured medially on longest tooth on the maxilla	
	Tooth length lower	tooth.l.l	Vertical distance from base of crown to tip of tooth measured medially on longest tooth on the mandible	
	Tooth thickness	tooth.th	Distance measured medially from the anterior proximal margin to the posterior proximal margin of the longest tooth	Inverse
	Upper tooth row length	row.len.u	Distance from the most proximal to most distal tooth insertions, measured on right side of maxilla	Square root
	Lower tooth row length	row.len.l	Distance from the most proximal to most distal tooth insertions, measured on right mandible	Square root
	Upper tooth row angle	row.ang.u	The externally visible angle between the left and right maxilla tooth rows	
	Lower tooth row angle	row.ang.l	The externally visible angle between the left and right mandibular tooth rows	Square root
	Oral disk width	disk.w	Maximum horizontal distance of the oral disk measured side to side, taken as zero if absent	Fourth root
	Oral disk length	disk.l	Maximum distance from anterior to posterior edge of the oral disk, taken as zero if absent	Fourth root
	Fleshy lip thickness	lip.th	Maximum distance from proximal to distal margin of fleshy lips	
	Number of pyloric caeca[†]	pyl.c	Number of individual pyloric caeca	
	Stomach length	stom.l	Maximum distance from anterior to posterior edge of stomach	Log

Table B 1. Continued.

Category	Trait	Code	Definition	Transformation[¥]
Trophic	Gut thickness[*]	gut.th	Thickness of stomach wall measured at mid-length	Log
	Stomach diameter	stom.d	Maximum diameter of empty stomach	Log
	Intestinal diameter	intest.d	Diameter of empty intestines measured at mid-length of the entire gut	Log

[¥]Variables that could not be normalized based on Shapiro Wilks Test were transformed to minimize skew
[†]Trait used only in Chapter II analysis
[*]Trait used only in Chapter III analysis

APPENDIX C

SPECIMEN LIST – CHAPTER III

Table C 1. List of specimens used in chapter III analyses. All specimens are deposited in the ichthyology collections of the Academy of Natural Sciences of Philadelphia (ANSP) and Instituto Nacional de Pesquisas Amazonica (INPA). Catalog numbers refer to lots of one or more individuals from the same sampling event; tissue numbers refer to unique identification tags for individual specimens within lots.

Family	Species	Catalog No.	Tissue No.*	Measurements†
Anostomidae	*Hypomasticus julii*	ANSP 194748	t0435	T, I
			t0436	T, I
			t0437	T, I
			t0438	I
			t0442	I
			t0444	I
	Leporinus sp. (16 circumpeduncle scales)	ANSP 194751	t0443	T, I
			t0447	T, I
			t0518	T, I
			t0519	I
		INPA 40204	t0445	I
			t0520	I
	Leporinus maculatus	ANSP 194750	t0517	T, I
		ANSP 194774	t0547	T, I
			t0548	I
		ANSP 194810	t0207	T
		ANSP 197383	t3040	I
	Leporinus aff. *fasciatus (Tapa-Xingu)*	ANSP 194817	NA	T
		ANSP 194900	t1160	T
			t1162	T
		INPA 40205	t0446	I
		INPA 40522	t1077	I
		INPA 40693	t1296	I
	Pseudanos trimaculatus	ANSP 194641	NA	T
			NA	T
			t1050	T, I
		INPA 40511	t1051	I
			t1048	I
			t1049	I
		INPA 40763	t1561	I
Apteronotidae	*Sternarchorhynchus* sp.	ANSP 194950	t1010	T, I
		INPA 40721	t1290	I
		ANSP 196430	t2254	T
		ANSP 196466	NA	T
Characidae	*Brycon* aff. *pesu*	ANSP 194652	NA	T

Table C 1. Continued.

Family	Species	Catalog No.	Tissue No.*	Measurements†
Characidae	*Brycon* aff. *pesu*	ANSP 194766	t0549	T
			t0550	T, I
		ANSP 197379	t3043	I
			t3044	I
	Moenkhausia heikoi	ANSP 194970	NA	T,
			t1515	T, I
			t1516	T, I
		INPA 40792	t1517	I
			t1519	I
Cichlidae	*Cichla pinima*	ANSP 194089	t1095	T
		ANSP 194454	t1194	T
		ANSP 194524	t1280	T, I
		INPA 40665	t1281	I
			t1282	I
	Crenicichla sp. (Xingu 1)§	ANSP 194647	t0124	T
		ANSP 194803	t0242	T
		ANSP 194995	NA	T
	Crenicichla sp. (Xingu 2)§	ANSP 194912	t0967	T
			t0968	T
		INPA 47729	t3100	I
		ANSP 196400	t2083	T
	Crenicichla sp. (Xingu 3)§	INPA 47728	t3099	I
	Crenicichla percna§	ANSP 197868	t3109	I
		INPA 47733	t3145	I
	Geophagus sp. (common high back)	ANSP 197513	t2329	T
			t2343	T
			t2349	T
		ANSP 194640	t1013	I
			t1015	I
			t1017	I
		ANSP 195155	t1298	I
	Teleocichla sp. (black)	ANSP 194828	t0266	T
		ANSP 194895	t1557	T, I
			t1556	I
		ANSP 194913	t0980	T
		ANSP 197831	t3615	I
			t3616	I
			t3617	I
			t3618	I

Table C 1. Continued.

Family	Species	Catalog No.	Tissue No.*	Measurements†
Ctenoluciidae	*Boulengerella cuvieri*	INPA 40798	t1573	I
		ANSP 195266	t2420	T
			t2421	T
			t2424	T
		INPA 52553	t3101	I
		ANSP 198237	t3123	I
Doradidae	*Platydoras* cf. *armatulus*	INPA 40527	t1067	I
			t1068	I
			t1069	I
		ANSP 194904	t1071	T, I
			t1073	T, I
			t1074	T, I
	Rhinodoras sp.	ANSP 194907	t1076	I
		INPA 40530	t1075	I
		ANSP 194808	t0248	T
		ANSP 194893	t1570	T, I
		INPA 40765	t1571	I
		ANSP 194907	t1076	T, I
		ANSP 194893	t1484	I
		INPA 40765	t1485	I
Hemiodontidae	*Hemiodus vorderwinkleri*	ANSP 194700	t1494	T, I
			t1495	T, I
		ANSP 194771	t0553	T
		INPA 40267	t0554	I
Loricariidae	*Acanthicus histrix*	INPA 40160	t0392	I
		ANSP 194953	t0995	I
			NA	T
			t0999	I
			t1001	I
		INPA 40452	t1000	I
		ANSP 194882	t1545	T, I
			t1547	T, I
	Ancistrus ranunculus	ANSP 194841	t0325	T, I
		ANSP 194955	t0907	T, I
		ANSP 194969	t1520	T, I
		INPA 40409	t0808	I
			t0811	I
			t0813	I
		ANSP 194417	t0812	I
	Baryancistrus xanthellus	ANSP 194814	t0212	T, I
		ANSP 194851	t0314	T, I
			t0334	T, I
		INPA 40187	t0475	I

Table C 1. Continued.

Family	Species	Catalog No.	Tissue No.*	Measurements†
Loricariidae	*Baryancistrus xanthellus*		t0477	I
		ANSP 194742	t0476	I
	Hopliancistrus tricornis	ANSP 194663	t0137	T, I
			t0138	T, I
			t0139	T, I
			t0140	I
			t0141	I
			t0142	I
	Hypancistrus sp. (L333)	ANSP 194643	t1041	T, I
			t1042	T, I
			t1046	T, I
		INPA 40739	t1371	I
		ANSP 194985	t1372	I
			t1373	I
	Hypostomus sp.	ANSP 194539	t1311	T, I
		ANSP 194649	t0161	T, I
		ANSP 194838	t0323	T, I
		INPA 40136	t0324	I
		INPA 40269	t0583	I
			t0584	I
	Leporacanthicus heterodon	ANSP 194749	t0458	T, I
		INPA 40201	t0459	I
			t0461	I
		ANSP 194870	t0938	T, I
		ANSP 194940	t0756	T, I
		INPA 40078	t0209	I
		ANSP 194798	t0210	I
	Panaqolus sp.	ANSP 194642	t1036	I
		INPA 40506	t1038	I
			t1039	I
		ANSP 194958	t1146	I
		ANSP 194631	t1255	T, I
			t1260	T, I
		ANSP 194790	NA	T
	Panaque armbrusteri	ANSP 194864	t0381	T, I
		ANSP 194759	t0527	I
		ANSP 194948	t1004	I
		INPA 40505	t1028	I
		ANSP 194890	t1567	T, I
			t1568	T, I
	Parancistrus aff. *aurantiacus*	ANSP 194495	t1524	T, I
		ANSP 194824	t0293	T, I
			t0294	T, I
		ANSP 194946	t0683	I

Table C 1. Continued.

Family	Species	Catalog No.	Tissue No.*	Measurements†
Loricariidae	*Parancistrus* aff. *aurantiacus*	INPA 40394	t0684	I
			t0685	I
	Peckoltia feldbergae	ANSP 194656	t0143	T, I
			t0144	T, I
		ANSP 194833	t0288	T, I
		ANSP 194991	t0399	I
		INPA 40180	t0400	I
			t0401	I
	Peckoltia sabaji	ANSP 194637	t1019	T, I
		ANSP 194846	t0330	T, I
		INPA 40148	t0331	I
		ANSP 194846	t0332	I
		INPA 40461	t0996	I
		ANSP 194891	t1550	T, I
	Peckoltia vittata	ANSP 194825	t0289	I
			t0290	I
		INPA 40283	t0595	I
		ANSP 194632	t1256	T, I
		ANSP 194638	t1026	T, I
			t1027	T, I
	Pseudacanthicus sp. (L25)	ANSP 194992	t0396	I
		INPA 40181	t0397	I
		ANSP 194906	t1079	T, I
			t1081	T, I
			t1083	T, I
		INPA 40846	t1626	I
	Pseudancistrus asurini	ANSP 194658	t0148	T, I
		ANSP 194848	t0311	I
		ANSP 194760	t0470	T, I
		ANSP 194878	t0941	I
			t0940	I
		ANSP 194892	t1463	T, I
	Scobinancistrus pariolispos	ANSP 194654	t0131	T, I
		INPA 40405	t0788	I
		ANSP 194915	t0786	I
		ANSP 194872	t0924	I
		ANSP 194894	t1551	T, I
		ANSP 194962	t1638	T, I
	Spatuloricaria tuira	ANSP 194651	t0183	T, I
		INPA 40120	t0281	I
			t0282	I
			t0283	I
		ANSP 194873	t0910	T, I

Table C 1. Continued.

Family	Species	Catalog No.	Tissue No.*	Measurements†
Loricariidae	*Spatuloricaria tuira*	ANSP 194939	t0754	T, I
	Spectracanthicus punctatissimus	ANSP 194552	t1314	T, I
			t1315	T, I
		ANSP 194834	t0297	T, I
		ANSP 194813	t0225	T, I
			t0226	T, I
		ANSP 194877	t0946	T, I
	Spectracanthicus zuanoni	ANSP 194812	t0215	T, I
			t0220	T, I
		ANSP 194944	t0686	I
		INPA 40391	t0687	I
			t0688	I
		ANSP 194944	t0741	T, I
Serrasalmidae	*Ossubtus xinguense*	ANSP 193060	NA	T,
		ANSP 194758	t0502	T, I
			t0505	T, I
		ANSP 194758	t0503	I
		INPA 40211	t0510	I
	Tometes kranponhah	ANSP 194419	t0805	T, I
		INPA 40430	t0806	I
			t0807	I
		ANSP 194763	t0514	T, I
			t0515	T, I

* NA values represent specimens for which a unique identifier was not assigned
† Individuals used for trait (T) or isotope (I) measurements
§ Due to insufficient sample sizes for any species of the genus *Crenicichla*, and high similarity of morphological and isotopic values, these species were pooled together (*Crenicichla* spp.) for the purpose of this analysis

APPENDIX D

RESULTS FOR WET-SEASON ASSEMBLAGES – CHAPTER III

Previous research on Xingu fishes found that functional diversity of wet-season assemblages was significantly underdispersed compared to null expectations along multiple niche axes (see Chapter II). Therefore, I expected no relationship between trait dispersion and trait association with trophic structure for these assemblages. Analysis included 29 species from six families due to seasonal turnover in species collected in main-channel habitats and followed methods described for dry-season communities.

Most metrics displayed no significant relationship with trait correlations with isotopic signatures (Fig. D1 and Table D1). Canonical ordination revealed that isotopic ratios explained a significant portion of the functional diversity ($F = 3.429$, $P = 0.002$; Adjusted $R^2 = 0.174$; Fig. D2), with significant effects of both $\delta^{15}N$ ($F = 4.39$, $P = 0.005$) and $\delta^{13}C$ ($F = 2.47$, $P = 0.047$). There was no significant difference between trait categories based on comparisons of mean correlation with $\delta^{15}N$ ($mean_{Habitat} = 0.297$, $mean_{Trophic} = 0.334$, $t = -0.68$, $P = 0.25$) or $\delta^{13}C$ ($mean_{Habitat} = 0.225$, $mean_{Trophic} = 0.238$, $t = -0.39$, $P = 0.35$; Fig. D3).

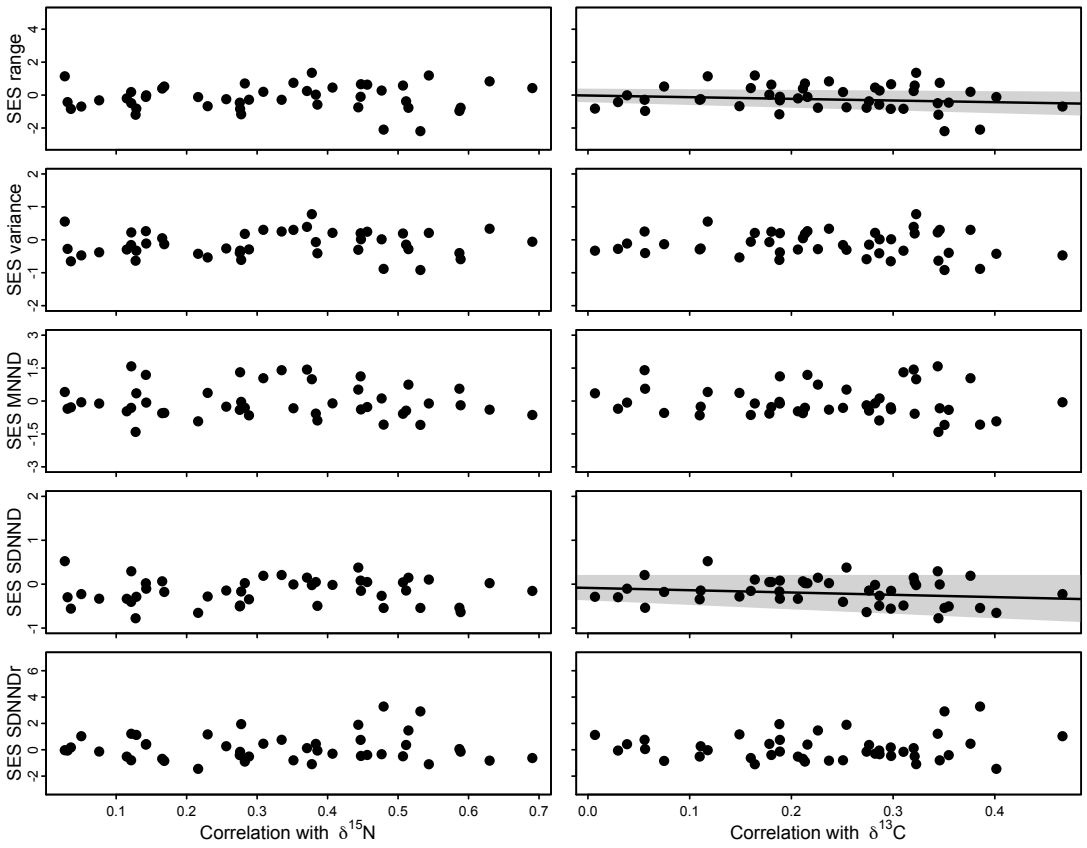

Figure D 1. Relationship between Standard Effect Size (SES) and spearman rank correlation with isotopic ratios of N ($\delta^{15}N$, left panel) and C ($\delta^{13}C$, right panel) for 45 morphological traits of wet-season assemblages. Points represent mean SES values across 23 sites. Black lines show mean trend for significant fixed effects of $\delta^{15}N$ and $\delta^{13}C$ based on linear mixed effects models with site included as a random intercept. Gray shaded regions represent 95% confidence intervals based on parametric bootstrapping. Abbreviations are for Mean Nearest Neighbor Distance (MNND), Standard Deviation of Nearest Neighbor Distance (SDNND), and SDNND/range (SDNNDr).

Table D 1. Results of linear mixed effects models for standard effect size (SES) of functional diversity measures in wet-season assemblages. Models fit by restricted maximum likelihood with $\delta^{13}C$ and $\delta^{15}N$ as fixed effects and site as a random intercept. Bold text indicates significant fixed effects based on parametric bootstrapped 95% confidence intervals (CI). Marginal ($_M$) and conditional ($_C$) R^2 values calculated following Nakagawa and Schielzeth (2013).

	$\delta^{15}N$		$\delta^{13}C$			
Response	Estimate (SE)	95% CI	Estimate (SE)	95% CI	R^2_M	R^2_C
range	0.32 (0.20)	(–0.08, 0.71)	**–1.01 (0.33)**	**(–1.66, –0.37)**	0.01	0.39
variance	0.21 (0.17)	(–0.11, 0.54)	–0.36 (0.27)	(–0.90, 0.14)	0.00	0.40
MNND	–0.21 (0.23)	(–0.66, 0.27)	–0.69 (0.38)	(–1.43, 0.12)	0.00	0.28
SDNND	0.14 (0.16)	(–0.17, 0.46)	**–0.52 (0.27)**	**(–1.05, 0.00)**	0.00	0.30
SDNNDr	0.04 (0.35)	(–0.65, 0.73)	0.95 (0.58)	(–0.18, 2.09)	0.00	0.14

Notes: MNND = mean nearest neighbor distance, SDNND = standard deviation of nearest neighbor distance. SDNNDr = standard deviation of nearest neighbor distance/range

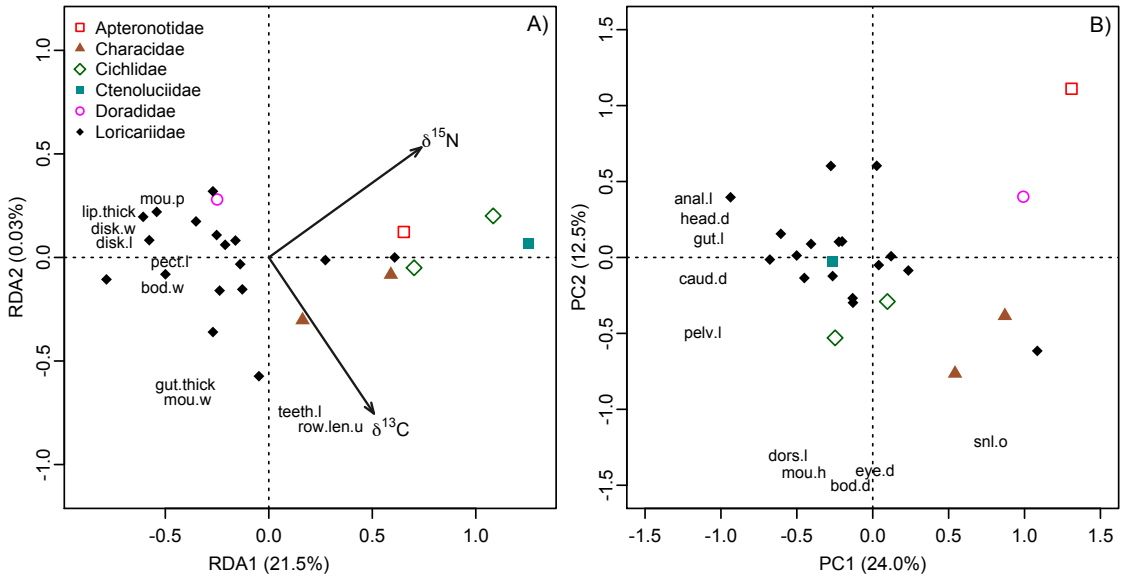

Figure D 2. Redundancy analysis of standardized morphological traits on standardized isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) for wet-season assemblages. Points are mean values for each species and symbols represent different families. Only traits with the 10 highest factor loadings are presented for clarity; trait abbreviations represent the apices of vectors originating from the origin. Arrows represent explanatory variables. Panel A) shows results of the constrained analysis plotted using the matrix of fitted values projected on the explanatory variables $\delta^{15}N$ and $\delta^{13}C$. Panel B) shows residual variation not accounted for by the RDA model. Trait abbreviations and descriptions are provided in *Appendix B*.

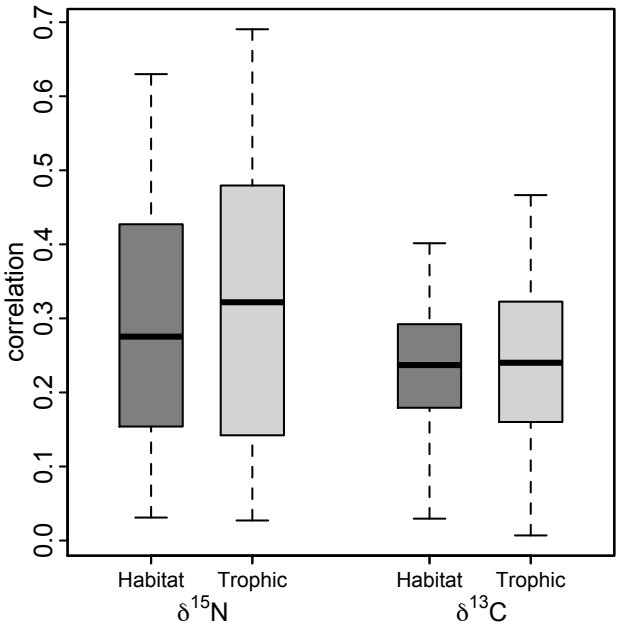

Figure D 3. Distributions of absolute value of spearman rank correlations between 45 morphological traits and isotopic ratios ($\delta^{15}N$ and $\delta^{13}C$) by trait category (Habitat and Trophic) for wet-season assemblages. For each element, mean values between categories are not significantly different based on a t-test.

APPENDIX E

SPECIES ABBREVIATIONS AND ABUNDANCES

Table E 1. Abbreviations and abundances for species collected within rapids of the Xingu River. Abundances are combined totals from the three survey periods (September 2013, March 2014, and November 2014)

Family	Species	Abbreviation	Abundance
Anostomidae	Anostomoides passionis	Ano pas	19
	Hypomasticus julii	Hyp jul	88
	Hypomasticus megalepis	Hyp meg	13
	Hypomasticus sp.	Hyp sp.4	2
	Laemolyta fernandezi	Lae fer	1
	Leporellus vittatus	Lep vit	20
	Leporinus desmotes	Lep des	3
	Leporinus fasciatus	Lep fas	14
	Leporinus friderici	Lep fri	1
	Leporinus maculatus	Lep mac	34
	Leporinus megalepis	Lep meg	6
	Leporinus tigrinus	Lep tig	9
	Petulanos intermedius	Pet int	9
	Pseudanos trimaculatus	Pse tri	13
	Rhytiodus argenteofuscus	Rhy arg	1
	Synaptolaemus cingulatus	Syn cin	3
	Synaptolaemus latofasciatus	Syn lat	5
	Synaptolaemus sp.	Syn sp.1	1
Apteronotidae	Adontosternarchus balaenops	Ado bal	3
	Apteronotus albifrons	Apt alb	1
	Apteronotus bonapartii	Apt bon	1
	Archolaemus janeae	Arc jan	1
	Sternarchorhamphus muelleri	Ste mue	2
	Sternarchorhynchus cf oxyrhynchus	Ste oxy	1
	Sternarchorhynchus higuchii	Ste hig	2
	Sternarchorhynchus kokraimoro	Ste kok	2
	Sternarchorhynchus mormyrus	Ste mor	1
	Sternarchorhynchus sp.	Ste sp.1	6

Table E 1. Continued.

Family	Species	Abbreviation	Abundance
Auchenipteridae	Auchenipterichthys longimanus	Auc lon	1
	Centromochlus aff simplex	Cen sim	4
	Centromochlus existimatus	Cen exi	37
	Centromochlus heckelii	Cen hec	18
	Centromochlus schultzi	Cen sch	20
	Tatia intermedia	Tat int	1
	Tatia musiaca	Tat mus	3
	Tatia simplex	Tat sim	5
	Tatia sp.	Tat sp.	1
	Tocantinsia piresi	Toc pir	2
	Tocantinsia sp.	Toc sp.	1
Callichthyidae	Corydoras sp. (C22)	Cor sp.1	36
	Corydoras xinguensis	Cor xin	18
Characidae	Astyanax guianensis	Ast gui	5
	Astyanax multidens	Ast mul	9
	Brycon aff pesu	Bry pes	7
	Brycon aff pesu (adiposa hialina)	Bry sp.1	117
	Brycon aff pesu (adiposa preta)	Bry sp.2	4
	Brycon falcatus	Bry fal	4
	Brycon pesu	Bry pes	45
	Brycon sp.	Bry sp.3	8
	Bryconamericus sp.	Bry sp.4	9
	Bryconops alburnoides	Bry alb	4
	Bryconops caudomaculatus	Bry cau	70
	Bryconops giacopinii	Bry gia	9
	Bryconops melanurus	Bry mel	4
	Creagrutus sp.	Cre sp.	4
	Hemigrammus manchinha	Hem man	5
	Hemigrammus ocellifer	Hem oce	2
	Hemigrammus sp.	Hem sp.	3
	Jupiaba acanthogaster	Jup aca	27
	Jupiaba cf essequibensis	Jup ess	5
	Jupiaba polylepis	Jup pol	48
	Knodus savannensis	Kno sp.3	9
	Knodus sp.	Kno sp.4	12
	Knodus sp. (dusky dorsal fin band)	Kno sp.1	82
	Knodus sp. (plain slender)	Kno sp.2	20

Table E 1. Continued.

Family	Species	Abbreviation	Abundance
Characidae	Microschemobrycon sp.	Mic sp.	5
	Moenkhausia celibela	Moe cel	5
	Moenkhausia ceros	Moe cer	7
	Moenkhausia collettii	Moe col	26
	Moenkhausia copei	Moe cop	26
	Moenkhausia cotinho	Moe cot	42
	Moenkhausia gr lepidura	Moe sp.1	3
	Moenkhausia gr lepidura (caudal spot varies)	Moe sp.2	42
	Moenkhausia gr lepidura (slender)	Moe sp.3	64
	Moenkhausia heikoi	Moe hei	45
	Moenkhausia lepidura	Moe lep	114
	Moenkhausia mikia	Moe mik	142
	Moenkhausia oligolepis	Moe oli	4
	Moenkhausia xinguensis	Moe xin	18
	Phenacogaster gr pectinatus	Phe pec	3
	Phenacogaster sp.	Phe sp.	11
	Rhinopetitia sp.	Rhi sp.2	40
	Roeboexodon guyanensis	Roe guy	4
	Tetragonopterus chalceus	Tet cha	1
Cichlidae	Aequidens michaeli	Aeq mic	3
	Caquetaia spectabilis	Caq spe	7
	Cichla melaniae	Cic mel	11
	Cichla pinima	Cic pin	3
	Crenicichla lugubris	Cre lug	1
	Crenicichla macropthalmus	Cre mac	12
	Crenicichla percna	Cre per	4
	Crenicichla preta	Cre pre	2
	Crenicichla reticulata	Cre ret	14
	Crenicichla sp.	Cre sp.4	4
	Crenicichla sp. (Xingu1)	Cre sp.1	18
	Crenicichla sp. (Xingu2)	Cre sp.2	16
	Crenicichla sp. (Xingu3)	Cre sp.3	68
	Crenicichla strigata	Cre str	1
	Geophagus argyrostictus	Geo arg	25
	Geophagus cf altifrons	Geo alt	7
	Geophagus sp.	Geo sp.2	11

Table E 1. Continued.

Family	Species	Abbreviation	Abundance
Cichlidae	Geophagus sp. (Acarai)	Geo sp.3	8
	Geophagus sp. (common high back)	Geo sp.1	26
	Geophagus sp. (split bar)	Geo sp.4	17
	Heros efasciatus	Her efa	2
	Retroculus xinguensis	Ret xin	11
	Symphysodon aequifasciatus	Sym aeq	4
	Teleocichla centisquama	Tel cen1	2
	Teleocichla centrarchus	Tel cen2	9
	Teleocichla gephyrogramma	Tel gep	11
	Teleocichla monogramma	Tel mon	52
	Teleocichla sp.	Tel sp.3	12
	Teleocichla sp. (CI)	Tel sp.1	63
	Teleocichla sp. (preta)	Tel sp.2	29
Crenuchidae	Characidium aff zebra	Cha zeb	3
	Melanocharacidium dispilomma	Mel dis	1
Ctenoluciidae	Boulengerella cuvieri	Bou cuv	8
	Boulengerella sp.	Bou sp.	2
Doradidae	Centrodoras brachiatus	Cen bra	4
	Centrodoras sp.	Cen sp.	29
	Hassar gabiru	Has gab	1
	Hassar orestis	Has ore	1
	Megalodoras sp.	Meg sp.1	2
	Megalodoras sp. (Xingu)	Meg sp.2	1
	Megalodoras uranoscopus	Meg ura	8
	Nemadoras ternetzi	Nem ter	1
	Platydoras armatulus	Pla arm	52
	Platydoras sp.	Pla sp.2	3
	Platydoras sp. (simple gas bladder)	Pla sp.1	9
	Pterodoras granulosus	Pte gra	1
	Rhinodoras sp.	Rhi sp.1	34
	Rhynchodoras xingui	Rhy xin	7
Erythrinidae	Hoplias curupira	Hop cur	1
Hemiodontidae	Bivibranchia fowleri	Biv fow	10
	Bivibranchia sp.	Biv sp.	5
	Hemiodus tocantinensis	Hem toc	10
	Hemiodus vorderwinkleri	Hem vor	17
Heptapteridae	Brachyglanis sp.	Bra sp.	1

Table E 1. Continued.

Family	Species	Abbreviation	Abundance
Heptapteridae	Cetopsorhamdia sp.	Cet sp.2	2
	Cetopsorhamdia sp. (Bockmann)	Cet sp.1	4
	Chasmocranus sp.	Cha sp.	1
	Leptorhamdia sp.	Lep sp.2	5
	Pimelodella cristata	Pim cri	1
Loricariidae	Acanthicus hystrix	Aca hys	33
	Acanthicus sp.	Aca sp.	3
	Acanthicus spinosus	Aca spi	1
	Ancistrus ranunculus	Anc ran	343
	Ancistrus sp.	Anc sp.1	251
	Ancistrus sp. (1)	Anc sp.2	3
	Ancistrus sp. (2)	Anc sp.3	1
	Ancistrus sp. (small white spots)	Anc sp.4	6
	Baryancistrus chrysolomus	Bar chr	32
	Baryancistrus niveatus	Bar niv	9
	Baryancistrus sp.	Bar sp.1	11
	Baryancistrus sp. (bolabranca)	Bar sp.2	33
	Baryancistrus sp. (verde)	Bar sp.3	371
	Baryancistrus xanthellus	Bar xan	442
	Curculionichthys cf sabaji	Cur sab	2
	Hisonotus sp.	His sp.	1
	Hopliancistrus sp. (Xingu)	Hop sp.	23
	Hopliancistrus tricornis	Hop tri	4
	Hypancistrus sp.	Hyp sp.3	116
	Hypancistrus sp. (marron)	Hyp sp.1	12
	Hypancistrus sp. (pao)	Hyp sp.2	478
	Hypancistrus zebra	Hyp zeb	8
	Hypoptopoma cf elongatum	Hyp elo	46
	Hypoptopoma inexpectatum	Hyp ine	23
	Hypostomus gr cochliodon	Hyp coc	4
	Hypostomus plecostomus	Hyp ple	1
	Hypostomus sp.	Hyp sp.5	5
	Leporacanthicus heterodon	Lep het	51
	Limatulichthys punctatus	Lim pun	1
	Limatulichthys sp.	Lim sp.1	4
	Limatulichthys sp. (nalto)	Lim sp.2	1

Table E 1. Continued.

Family	Species	Abbreviation	Abundance
Loricariidae	Loricaria birindellii	Lor bir	5
	Loricaria gr cataphracta	Lor cat	3
	Loricaria sp.	Lor sp.	2
	Oligancistrus sp.	Oli sp.1	166
	Oligancistrus sp. (dorsal negra)	Oli dor	2
	Oligancistrus sp. (micropunctatus)	Oli sp.3	1
	Panaqolus sp.	Pan sp.	310
	Panaque armbrusteri	Pan arm	87
	Parancistrus nudiventris	Par nud	287
	Parancistrus sp.	Par sp.2	25
	Parancistrus sp. (no spots)	Par sp.1	2
	Parancistrus sp. (uniformly dark)	Par sp.3	35
	Parotocinclus sp.	Par sp.4	5
	Peckoltia feldbergae	Pec fel	96
	Peckoltia sabaji	Pec sab	73
	Peckoltia vittata	Pec vit	326
	Pseudacanthicus sp.	Pse sp.3	14
	Pseudacanthicus sp. (black)	Pse sp.1	8
	Pseudacanthicus sp. (L25)	Pse sp.2	9
	Pseudancistrus asurini	Pse asu	77
	Pseudancistrus sp.	Pse sp.4	22
	Pseudoloricaria laeviuscula	Pse lae	1
	Rineloricaria sp.	Rin sp.	1
	Scobinancistrus aureatus	Sco aur	124
	Scobinancistrus pariolispos	Sco par	60
	Scobinancistrus sp.	Sco sp.1	5
	Scobinancistrus sp. (tubarao)	Sco sp.2	6
	Spatuloricaria sp.	Spa sp.	14
	Spatuloricaria tuira	Spa tui	29
	Spectracanthicus immaculatus	Spe imm	17
	Spectracanthicus punctatissimus	Spe pun	714
	Spectracanthicus punctatissimus (bola marron)	Spe sp.1	7
	Spectracanthicus punctatissimus (long snout)	Spe sp.2	19
	Spectracanthicus punctatissimus (short snout)	Spe sp.3	27

Table E 1. Continued.

Family	Species	Abbreviation	Abundance
Loricariidae	Spectracanthicus zuanoni	Spe zua	558
	Squaliforma sp.	Squ sp.1	48
	Squaliforma sp. (Xingu)	Squ sp.2	11
Pimelodidae	Brachyplatystoma tigrinum	Bra tig	1
	Pimelodus ornatus	Pim orn	1
	Pimelodus sp.	Pim sp.	1
	Pinirampus pirinampu	Pin pir	1
	Platystomatichthys sturio	Pla stu	1
	Propimelodus eigenmanni	Pro eig	3
	Propimelodus sp.	Pro sp.	1
Potamotrygonidae	Paratrygon aiereba	Par aie	1
	Potamotrygon leopoldi	Pot leo	5
	Potamotrygon motoro	Pot mot	1
	Potamotrygon scobina	Pot sco	2
Pseudopimelodidae	Pseudopimelodus cf bufonius	Pse buf	3
Pseudopimelodidae	Pseudopimelodus pulcher	Pse pul	5
	Pseudopimelodus sp.	Pse sp.5	2
	Batrochoglanis sp.	Bat sp.	1
Sciaenidae	Pachypops sp.	Pac sp.	1
	Pachyurus schomburgkii	Pac sch	2
	Petilipinnis grunniens	Pet gru	1
Serrasalmidae	Myloplus arnoldi	Myl arn	4
	Myloplus schomburgkii	Myl sch	4
	Myloplus sp.	Myl sp.	1
	Ossubtus xinguense	Oss xin	21
	Pristobrycon striolatus	Pri str	1
	Serrasalmus manueli	Ser man	3
	Serrasalmus rhombeus	Ser rho	1
	Tometes kranpohnah	Tom kra	214
Sternopygidae	Sternopygus sp.	Ste sp.2	3
Synbranchidae	Synbranchus sp.	Syn sp.8	7
	Synbranchus sp. (boldly spotted)	Syn sp.2	1
	Synbranchus sp. (dark mottled)	Syn sp.3	2
	Synbranchus sp. (deep head)	Syn sp.4	4
	Synbranchus sp. (dusky mottled)	Syn sp.5	1
	Synbranchus sp. (herringbone)	Syn sp.6	1

Table E 1. Continued.

Family	Species	Abbreviation	Abundance
Synbranchidae	Synbranchus sp. (irregularly spotted)	Syn sp.7	5
	Synbranchus sp. (uniformly dusky)	Syn sp.9	2
Trichomycteridae	Vandellia sp.	Van sp.	33
Triportheidae	Triportheus albus	Tri alb	3

APPENDIX F

SUPPLEMENTARY FIGURES – CHAPTER IV

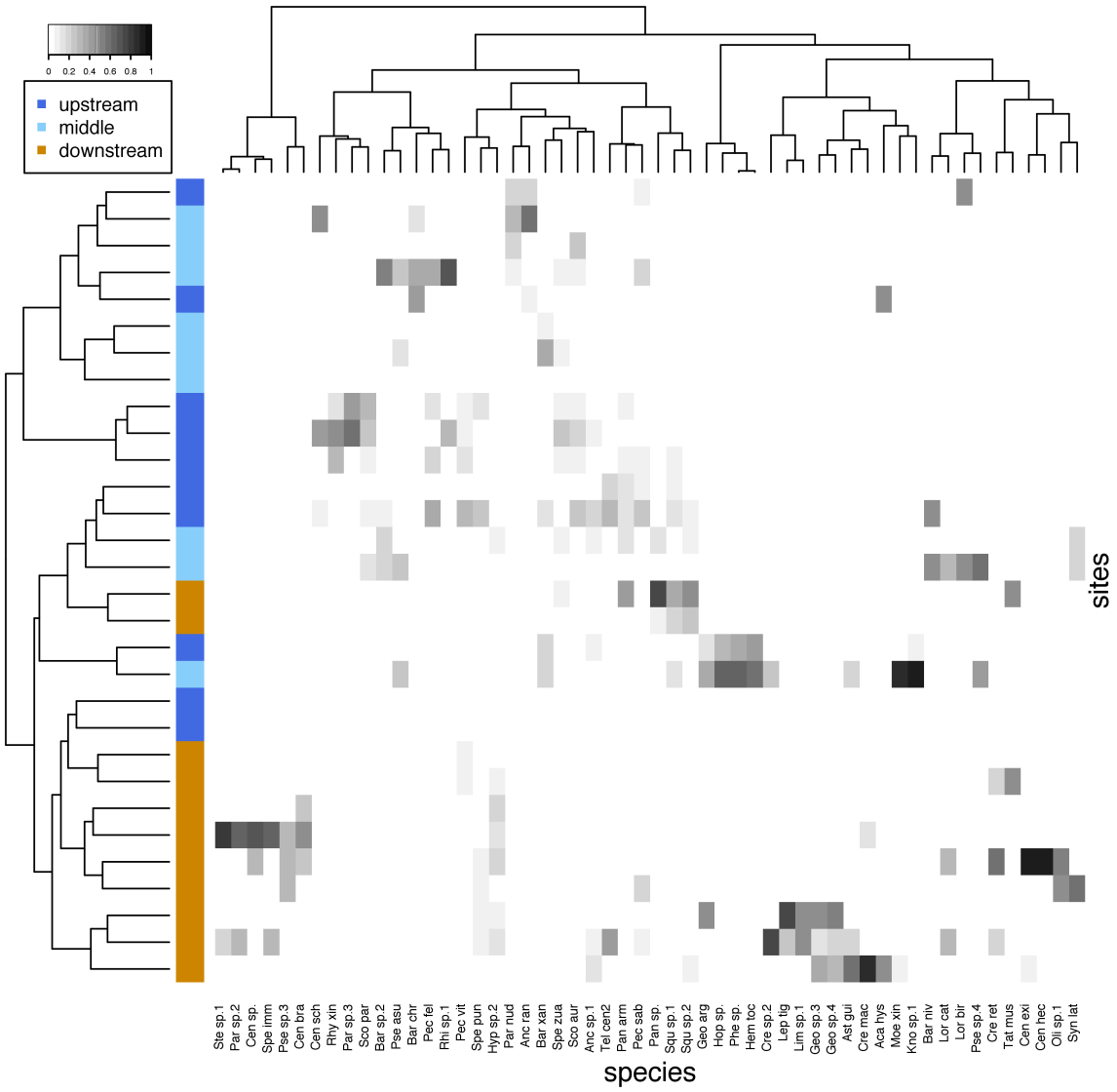

Figure F 1. Two way cluster analysis of high-water (March 2014) assemblages. Clustering follows Ward's D, using Bray-Curtis dissimilarity matrix based on species relative abundances. Colors along edge represent river sections and grey-scale shading within represents species relative abundance at a given site.

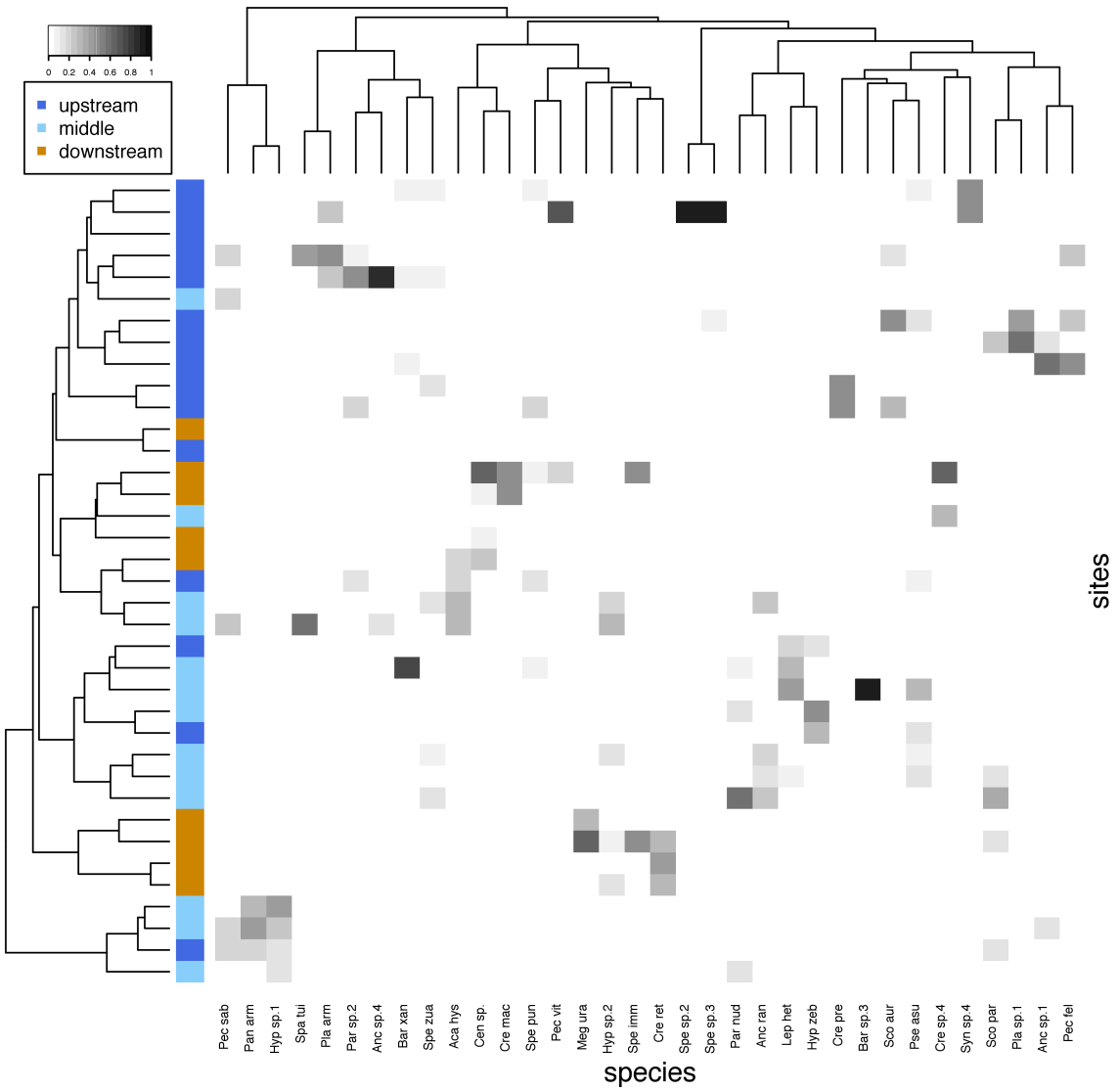

Figure F 2. Two-way cluster analysis of low-water (November 2014) assemblages. Clustering follows Ward's D, using Bray-Curtis dissimilarity matrix based on species relative abundances. Colors along edge represent river sections and grey-scale shading within represents species relative abundance at a given site**.**

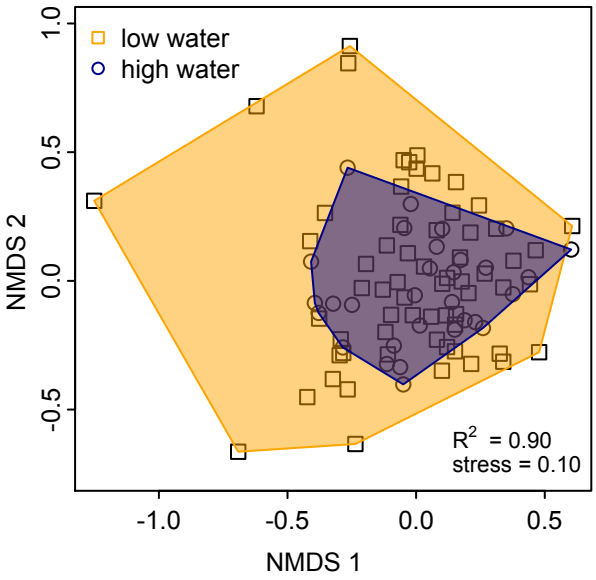

Figure F 3. Non-metric multidimensional scaling results comparing low- and high-water sites based on species relative abundance at sampling sites. Low-water sites combine September 2013 and November 2014 surveys. High-water sites surveyed in March 2014. Symbols represent sites and shaded polygons are convex hulls for each season.